Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 113, No. 1

A MONOGRAPHIC REVISION OF THE ANT GENUS *LASIUS*

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With Two Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
March, 1955

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INTRODUCTION

Lasius is one of the most prominent and familiar of the Holarctic ant genera. From the time of Réaumur in the eighteenth century (Wheeler, 1926), European and North American entomologists have focused attention on it in countless general biological and taxonomic investigations which are today part of the classical foundation of myrmecology. It is probably best known for its conspicuous nuptial flights, its habit of tending and transporting homopterous insects, and the temporary parasitic behavior of some of its species. It has also attracted much attention as one of the several ant genera which have persisted in Europe and North America since early Tertiary times with only a small amount of visible evolutionary change.

Today it occupies a purely Holarctic range. Northward it reaches northern Scandinavia, the Baikal region of Siberia, Kamchatka, southeastern Alaska, and southern Labrador. Southward it reaches Madeira, North Africa, northern Iraq, the southern Himalayas, the mountains of Formosa, the mountains of central Mexico, and northern Florida. Where it comes closest geographically to tropical faunas, as in southeastern Asia, it still retains its north-temperate character, i.e., limited to temperate vegetation at higher elevations and there associated chiefly with typically Holarctic ant genera.

Within this range it is among the most abundant of all insect genera. In Europe the two species *niger* and *flavus* are often the overriding dominants of the ant fauna in local situations and under a variety of ecological conditions. In the eastern United States *L. neoniger* (=*L. niger americanus div. auct.*) mounts such dense populations in open fields and lawns that W. M. Wheeler was once moved (1905) to suggest that it might be the most abundant insect in North America. Such a contention would probably be an exaggeration with respect to all insects, of course, yet there is no denying *neoniger* its importance as a major faunal influent within its range and favored habitat.

Despite the great prominence of this genus, the taxonomy of *Lasius,* like that of most ant genera, has been a sorry shambles. In particular, there have been no keys that work satisfactorily; those in the literature today will not suffice to determine even the type specimens of many species. A principal reason for this condition is that some of the best diagnostic characters in the genus involve structures hitherto ignored. Furthermore, the nomenclature has been badly complicated by an excessive accumulation of poorly defined forms, mostly of a trivial infraspecific nature. Out of the 110 unchallenged names which existed in the literature at the outset of this revision, I have been able to establish only 27 as representing valid species (not counting the six additional new species). The others patently serve only to obscure the true picture of intraspecific variation and to render clearcut species diagnoses impossible. Finally, the situation has been aggravated by the hitherto unsuspected presence of a number of cryptic species closely related to some of the most common members of the genus. Formerly lumped with their named siblings, they have had the effect of broadening and confusing species diagnoses. Creighton (1950), for instance, recognizes only two forms of the subgenus *Lasius* in North America, "*niger neoniger*" and "*alienus americanus*", which he and others have separated principally by a single character in pilosity. Actually, these two names apply to six distinct species in North America: *sitkaensis* Pergande, *niger* (Linnaeus), *alienus* (Foerster), *neoniger* Emery, *crypticus* Wilson, and *sitiens* Wilson, each abundant and widely distributed. It is impossible to make a two-way split in this group on the basis of the pilosity character, since in this respect *sitkaensis* by itself brackets all of the variation shown by the other species. The taxonomy of the group was finally solved in the course of the present study by reference to other characters in dentition, clypeal outline, etc., combined with trends in pilosity.

Beyond the urgent need for a purely taxonomic revision, *Lasius* has presented many excellent opportunities for studies of more general nature. Chief among its advantages in this respect is the large amount of available material, which has allowed extensive statistical descriptions and analyses. I have been able in the course of only two years to gather and examine an estimated total of 5,425 nest series containing approximately 80,000 specimens. Not every specimen in every nest series was studied microscopically, but all were at least cursorily checked, and contributed to overall impressions of variability in size, color, and habitus. *Lasius* is also remarkable — perhaps unique — among animal groups thus far monographed, in its great abundance, ubiquity, and conspicuousness, and the consequent ease with which it can be found in the field. Anywhere in the northern United States, in practically all but desert and semidesert conditions, it is possible for an investigator to walk onto nearly any plot of ground and within a matter of minutes find nests of one or more species. As a result, surveys of population density and comparative ecology can be conducted swiftly and easily.

REFERENCE COLLECTIONS

During the course of this study collections of *Lasius* from many sources have been handled, and nest series divided and redistributed in such a way as to allow an efficient dispersal of duplicate type and determined material. At the present time the single most important reference collection is that of the Museum of Comparative Zoology of Harvard University. I have made an effort to concentrate here nest duplicates of all of the significant series in this study, including types, and have succeeded in building substantial collections of all but the rarest species. This material will be available to check possible errors in the revision, and will provide a starting point for future studies of a similar nature. Below are listed other institutions and private collections (the latter under the collector's name) which are considered important by virtue of their containing types and critical determined material. They are accompanied by the abbreviations used to designate them in the descriptive parts that follow.

Academy of Natural Sciences, Philadelphia (ANSP).
American Museum of Natural History, New York City (AMNH).
Zoologisches Museum der Universität, Berlin (Berlin Museum).
Mr. Michel Bibikoff, Leamington Spa, England (Bibikoff Coll.).
Bondroit Collection, Institut Royal d'Histoire Naturelle de Belgique, Brussels (Bondroit Coll.).
British Museum (Natural History), London.
California Academy of Sciences, San Francisco (CAS).
Dr. A. C. Cole, University of Tennessee, Knoxville (Cole Coll).
Dr. W. S. Creighton, City College of New York (Creighton Coll.).
Emery Collection, Museo Civico di Storia Naturale, Genoa (Emery Coll.).
Forel Collection, Muséum d'Histoire Naturelle, Geneva (Forel Coll.).
Docent Karl-Herman Forsslund, Skogsforskningsinstitut, Experimental fältet, Sweden (Forsslund Coll.).
Dr. Holger Holgersen, Stavanger Museum, Stavanger, Norway (Holgersen Coll.).
Illinois State Natural History Survey, Urbana (INHS).
Dr. Robert L. King, University of Iowa, Iowa City (King Coll.).
Dr. Heinrich Kutter, Flawil, Switzerland (Kutter Coll.).
Mayr Collection, Naturhistorisches Museum, Vienna (Mayr Coll.).
Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (MCZ). Includes W. M. Wheeler and B. Finzi Collections.

Mr. H. Okamoto, care of Dr. K. Yasumatsu, address below (Okamoto Coll.).

Santschi Collection, Naturhistorisches Museum, Basel, Switzerland (Santschi Coll.).

Schenck Collection, Zoologisches Museum der Universität, Marburg, Germany.

Snow Entomological Museum, University of Kansas, Lawrence.

Dr. Mary Talbot, Lindenwood Côllege, St. Charles, Missouri (Talbot Coll.).

United States National Museum, Washington, D. C. (USNM).

University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

Dr. N. A. Weber, Swarthmore College, Swarthmore, Pennsylvania (Weber Coll.).

Dr. G. C. Wheeler, University of North Dakota, Grand Forks (G. C. Wheeler Coll.).

W. M. Wheeler Collection, see Museum of Comparative Zoology.

Dr. Keizô Yasumatsu, University of Kyushu, Fukuoka (Yasumatsu Coll.).

ACKNOWLEDGMENTS

This study was made possible by the cooperation of many European, Japanese, and American entomologists who have contributed specimens and ecological information from over the entire range of *Lasius*. It has been primarily through their efforts that I have been able to examine the largest amount of material ever assembled for a revision of any group of ants, and one excelled by few other collections of special insect groups. Professor K. Yasumatsu and Mr. H. Okamoto of Japan made available from their collections what is probably several times over the number of nest series of *Lasius* seen by all non-Japanese myrmecologists in the past. Dr. G. C. Wheeler sent the enormous collection which he and his students have been gathering from the North Dakota area for the past twenty-five years, containing the impressive sum of over 900 nest series and many tens of thousands of individual specimens. Others have lent their personal collections or the institutional collections in their charge to swell by at least tenfold the number of series which were initially available in the Museum of Comparative Zoology and my own collection. Space does not permit me to detail the material and help received from every person; I can only list their names, along with their addresses or the reference collection with which they are associated, and express to each my sincere appreciation for their cooperation.

Prof. R. H. Beamer (Snow Entomological Museum, University of Kansas); Dr. M. Beier (Mayr Coll.); Mr. Michel Bibikoff (Bibikoff Coll.); Dr. M. V. Brian (The University, Glasgow, Scotland); Dr. H. Bischoff (Berlin Museum); Dr. Charles Bisgaard (Zoologisk Museum, Copenhagen); Dr. W. L. Brown (MCZ); Dr. L. F. Byars (U. S. Public Health Service, Savannah, Georgia); Prof. F. M. Carpenter (MCZ); Dr. Kenneth Christiansen (American University of Beirut, Lebanon); Dr. A. C. Cole (Cole Coll.); Monsieur A. Collart (Bondroit Coll.); Mr. C. A. Collingwood (Evesham, Worcestershire, England); Dr. T. W. Cook (Oakland, California); Dr. W. S. Creighton (Creighton Coll.); Dr. Ch. Ferrière (Forel Coll.); Docent K.-H. Forsslund (Forsslund Coll.); Prof. S. W. Frost (Pennsylvania State University); Mr. N. Gillham (MCZ); Dott. Delfa Guiglia (Emery Coll.); Prof. Ed. Handschin (Santschi Coll.); Dr. Holger Holgersen (Holgersen Coll.); Mr. P. B. Kannowski (UMMZ); Dr. R. L. King (King Coll.); Prof. C. Kosswig (Zoologi Enstitüsü, Müftülük Binasinda, Istanbul); Mr. Kenneth Kraft (University of North Dakota, Grand Forks); Dr. Masao Kubota (Odawara, Kanagawa Pref., Honshu); Dr. Heinrich Kutter (Kutter Coll.); Mr. W. E. LaBerge (University of Kansas, Lawrence); Mr. Borys Malkin (Malkin Coll.); Dr. W. L. Nutting (Biological Laboratories, Harvard University, Cambridge, Massachusetts); Mr. H. Okamoto (Okamoto Coll.); Dr. Fergus J. O'Rourke (University of Cork, Eire); Dr. Orlando Park (Northwestern University, Evanston, Illinois); Dr. Albert Raignier (Institut de Zoologie, Louvain, Belgium); Dr. E. S. Ross (CAS); Dr. M. R. Smith (USNM); Dr. L. J. Stannard (INHS); Dr. Mary Talbot (Talbot Coll.); Mr. Ernest Taylor (Oxford University Museum, England); Mr. B. D. Valentine (Biological Laboratories, Harvard University, Cambridge, Massachusetts); Father Joseph van Boven (Roermond, Holland); Dr. A. F. Van Pelt (Appalachian State Teachers College, Boone, North Carolina); Dr. N. A. Weber (Weber Coll.); Dr. G. C. Wheeler (G. C. Wheeler Coll.); Dr. I. H. H. Yarrow (British Museum); Dr. Keizô Yasumatsu (Yasumatsu Coll.).

In addition, I would like to make special acknowledgments to

two men who in personal contact with the writer have had a major influence in the shaping of this study and deserve a large part of the credit for whatever success it may enjoy. Dr. W. L. Brown has followed the revision step by step and drawn upon his truly great knowledge of ants to help guide the work through its most difficult phases. There are doubtless errors remaining in this work but they are much fewer than in the original drafts thanks to his painstaking and enlightened inquiry into nearly every detail. Prof. F. M. Carpenter has made possible the work on the fossil species by arranging the loan of the Museum of Comparative Zoology collections and directing the writer in their preparation and examination. But he has been even more helpful as my graduate sponsor at Harvard, in which role he has always been most thoughtful and graciously patient.

I would also like to express appreciation to Prof. Ernst Mayr for his effective and penetrating advice on certain matters of taxonomic procedure and theory; to Miss Ruth Dunn for her aid in the translation of Russian scientific papers; to Dr. W. L. Nutting and Mr. Thomas Eisner for aid in field work and preparation of illustrations; and to Miss Janice Cassani for aid in the preparation of the final manuscript.

Field work in the summer of 1952 was supported in part by a grant-in-aid from Sigma Xi-RESA.

GENERIC STATUS AND SUBGENERA

Lasius as originally conceived by Fabricius (1805) contained two species which are recognizable at the present time, *niger* (Linnaeus) and *emarginatus* (Olivier). The generic name *Lasius* was not used consistently, however, until Mayr (1861) revived it and set up the limits recognized today. In 1903 Bingham designated *niger* as the generitype. Some disorder was introduced in 1914 when Morice and Durrant called attention to an early paper by Jurine (1801) in which the name *Lasius* had been proposed for a genus of bees prior to Fabricius' publication. For the ant genus they created the name *Donisthorpea*, with *niger* as the generitype. This unfortunate nomenclatural maneuver precipitated a great deal of debate among ant specialists and began a lengthy period during which several names (*Lasius*, *Acanthomyops, Formicina, Donisthorpea*) were used for the genus simultaneously. The historical details have been reviewed by Donisthorpe (1927) and Creighton (1950) and for practical purposes are now largely irrelevant. It is sufficient to say that in 1935 the International Commission of Zoological Nomenclature ruled Jurine's publication invalid and restored *Lasius* to the ants. Among ant taxonomists, in recent years, only Donisthorpe refused to accept this ruling and continued to use the name *Donisthorpea.*

DIAGNOSIS. The species of *Lasius* belong to the subfamily Formicinae, section Euformicinae (*sensu* Emery, 1925). They belong with the group of genera comprising Emery's 1925 concept of the closely related (and possibly inseparable) tribes Lasiini and Formicini. Within the orbit of these genera, *Lasius* can be characterized as follows: Size small to medium; worker and queen bodies robust, with heads massive relative to the alitrunk; palpal segmentation 6, 4 (except in males of *Dendrolasius,* the terminal palpal segments of which exhibit variable and irregular ankylosis); worker and queen mandibles with 7 to 12 teeth following the typical formicine pattern (as defined on p. 000; a single exception is found in the queen of *L. carniolicus,* which has reduced dentition), primitively with one or more offset teeth at the basal angle; male mandible primitively with a narrow preapical cleft, a well defined basal angle, and anterior masticatory denticles; worker alitrunk not conspicuously constricted or otherwise specialized, the mesonotum typically convex in side view; propodeal spiracle round; petiolar scale in side view prominent, erect, and typically symmetrical; male genitalia generalized but weakly developed.

The closest living relative of *Lasius* is the Nearctic genus *Acanthomyops,* which is believed to be a temporary social parasite on some *Lasius* members. *Acanthomyops* differs consistently only in its reduced palpal segmentation (formula—3, 4). In other characters, including habitus and pilosity, it is overlapped by members of the subgenus *Lasius* (*Chthonolasius*), which is most likely its direct ancestor. Beyond this one sound phylogenetic link, the affinities of *Lasius* are difficult to ascertain. The mandible form of its primitive members is the most generalized encountered within the Lasiini and Formicini, and may represent the prototypic condition for the Formicinae as a whole. The genera ordinarily bracketed with *Lasius*—*Prenolepis,* *Paratrechina,* and *Pseudolasius* — show considerable modifications in mandibular structure, pilosity, and body form which set them well apart from this genus. On the other hand, *Formica* is generalized in the same characters as *Lasius* and may be closer to it, despite several striking specializations in the male. Future revisionary work will probably necessitate either the incorporation of the Lasiini into the Formicini, or the division of this tribal complex along different lines than those now recognized.

LASIUS Fabricius

Lasius Fabricius, 1805, Systema Piezatorum, p. 415. Generitype: *Formica nigra* L., designated by Bingham, 1903, The Fauna of British India, **2:** 338.

Formicina div. auct., nec Shuckard, 1840 (generitype *Formica rufa* L., designated by Wheeler, 1911, Ann. New York Acad. Sci., **21:** 164).

Acanthomyops div. auct., nec Mayr, 1862 (generitype *Formica clavigera* Roger, by monotypy), *part.*

Donisthorpea Morice and Durrant, 1914, Trans. Roy. Ent. Soc. London, pp. 421–423. Generitype: *Formica nigra* L., by original designation.

Subgenus LASIUS Fabricius

DIAGNOSIS. Queen non-parasitic, the head width much less than the width of the thorax just in front of the tegulae. Worker eye length at least 0.20 × the head width, and usually more. In all three castes the metapleural gland is not reduced, i.e., the greatest width of the gland opening measured perpendicular to its long axis is greater than the maximum length of the propodeal spiracle, including the darkened rim. Worker body color usually light to blackish brown, rarely yellowish brown. Maxillary palp segments V and VI typically subequal in length to segment IV, and length of segment VI typically exceeding 0.14 × the head width. Male mandible showing interspecific variation from the most primitive type in the genus (*sitkaensis*) to the most advanced (*niger* complex). *Lasius sitiens* Wilson is intermediate to the subgenus *Cautolasius* in its lightened body color, reduced eye size, and shortened terminal maxillary palp segments (length of segment VI 0.12-0.14 × the head width), but these are obviously secondary modifications. The closest relative of *sitiens,*

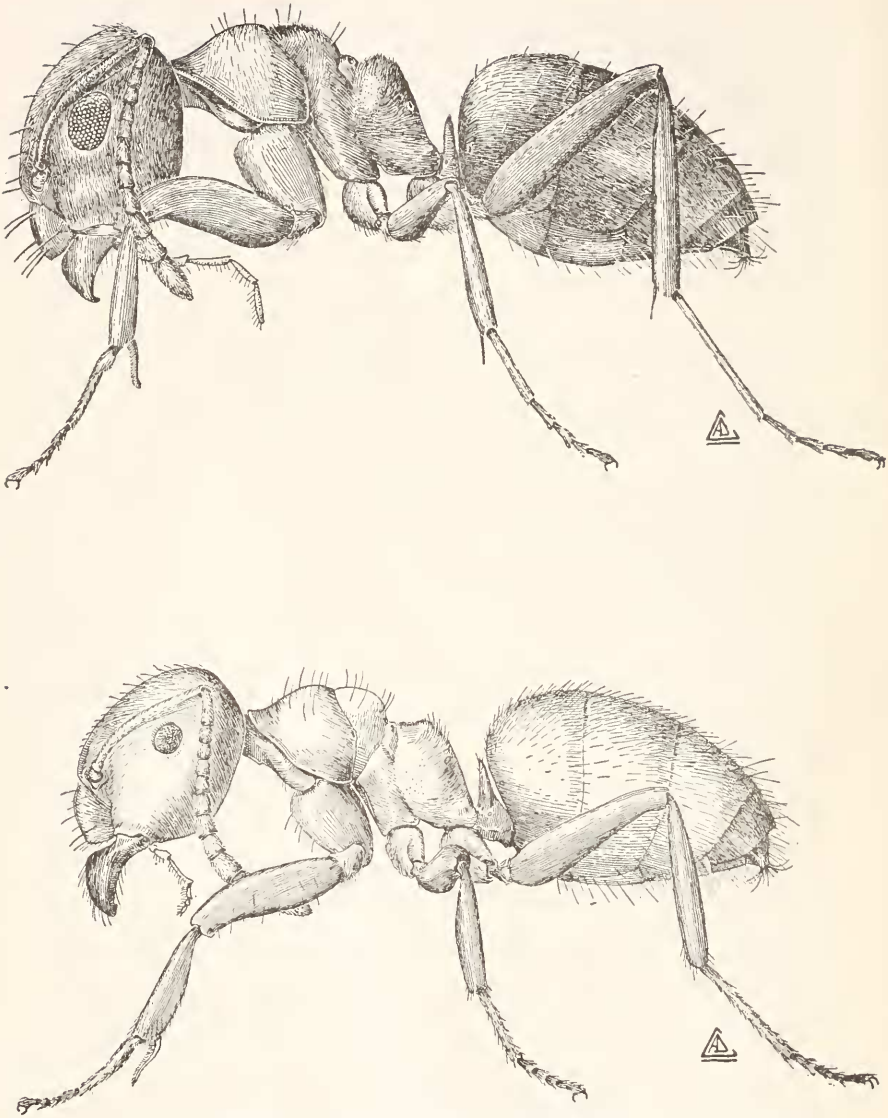

Fig. 1. *Above,* worker of *Lasius* (*Lasius*) *alienus* (Foerster). *Below,* worker of *Lasius* (*Chthonolasius*) *umbratus* (Nylander). Both specimens from North America. Original by A. D. Cushman, courtesy of M. R. Smith.

L. crypticus Wilson, shows a similar shortening of the maxillary palps, and both are connected in this character to the remainder of the subgenus by the more generalized species *L. neoniger* Emery. (See Fig. 1.)

Subgenus CAUTOLASIUS Wilson, new subgenus

Subgeneritype: FORMICA FLAVA Fabricius, by present selection.

I propose to separate the members of the *flavus* complex — *flavus* (Fabricius), *nearcticus* Wheeler, *alienoflavus* Bingham, *talpa* Wilson, and *fallax* Wilson — as a distinct subgenus. This group of species is closely knit and shows a mixture of characters which on purely morphological grounds places it in a position intermediate between *Lasius s. s.* and *Chthonolasius*. The worker caste closely resembles that of *Chthonolasius,* in having light body color, reduced eye size, and shortened maxillary palps. However, these are most likely convergent characters developed in connection with a common subterranean mode of life. The closest affinities of *Cautolasius* are to *Lasius s. s.,* and it was probably derived from the latter subgenus. The queen is nonparasitic and very similar to *Lasius s. s.* in habitus, with the head small relative to the thorax. In all three castes the opening of the metapleural gland is as large as in *Lasius s. s.* Male mandible showing the maximum range of variation for the genus (*sitkaensis* to *niger* types), within a single species (*flavus*). The most primitive member of the subgenus, *L. alienoflavus* Bingham, has terminal maxillary palp segments fully as long as those of *L.* (*L.*) *sitiens* Wilson, while the color variation of *L. flavus* overlaps that of *sitiens*. In final analysis the only character which by itself will separate the two subgenera is eye size. Yet the two still represent discrete groups, since *sitiens* is a secondarily specialized member of a phylogenetically remote species group.

Subgenus CHTHONOLASIUS Ruzsky

Chthonolasius Ruzsky, 1913, Arch. Naturgesch., **79**(A9): 59–61. Subgeneritype: *Formica umbrata* Nylander, by designation of Emery, 1925, Genera Insect., fasc. 183, p. 232.

DIAGNOSIS. Queen temporarily parasitic on species of *Lasius s. s.;* the head width about as great as the width of the thorax just anterior to the tegulae or greater. Worker eye length never more than 0.17 × the head width and usually less. Metapleural gland reduced in all three castes, so that the gland opening measured perpendicular to the long axis is less than the maximum length of the propodeal spiracle, including the darkened rim. Worker color light yellow to light yellowish brown. Maxillary palp segments V and VI conspicuously reduced relative to IV, the length of VI typically not exceeding 0.10 × the head width. Pilosity often highly specialized, apparently as a parasitic coadaptation. Male mandible of the primitive *sitkaensis* type. The following larval characters have been established in the present study: relative to *Lasius s. s.* (*sitkaensis, alienus*) and *Cautolasius* (*flavus*), the *Chthonolasius* head is more slender and the external mandibular borders more convex (see figures in G. C. Wheeler, 1953, p. 153). (See Fig. 1.)

Subgenus DENDROLASIUS Ruzsky

Dendrolasius Ruzsky, 1913, Arch. Naturgesch., **79**(A9): 59. Generitype by monotypy: *Formica fuliginosa* Latreille.

DIAGNOSIS. Queen head width and worker eye size as in *Chthonolasius.* Metapleural gland reduced in the queen and male and, unlike the other subgenera, lacking guard hairs; yet well developed and with guard hairs in the worker. The scutum of the queen in side view overhangs the pronotum and contributes all of the anterior alitruncal convexity, whereas in the other subgenera it shares the convexity with the pronotum. Worker color jet black. Maxillary palp segments V and VI subequal to IV, but the entire palp reduced in size, so that VI does not exceed in length 0.12 × the head width. Male mandible of the advanced *niger* type.

PHYLOGENY WITHIN THE GENUS

I have represented in the diagram of Figure 2 my own conception of the phylogenetic deployment of the species of *Lasius.* All evidence points to *L. sitkaensis* Pergande, a boreal Nearctic species, as the most generalized member of the genus. First, it carries the characters of the subgenus *Lasius,* which is morphologically and ethologically the most generalized of the four subgenera. Second, *sitkaensis* possesses characters in the mandible form which appear, both in the female and male, to be end points of independent morphoclines. The offset basal tooth of the female is not shared by any other *Lasius s. s.* or *Cautolasius* (a similar structure of doubtful homology occurs occasionally in the queen of *L. neoniger* Emery, *q. v.*), but it is characteristic of *Dendrolasius* and appears sporadically on *L. umbratus* (*Nyl.*), which species is in other characters the most generalized member of *Chthonolasius*. The form of the male mandible ("*sitkaensis* type", p. 37) is shared with *Chthonolasius; Cautolasius* shows within its membership all gradations from this type to the "*niger* type"; *L.* (*L.*) *brunneus* (Latr.) has an intermediate

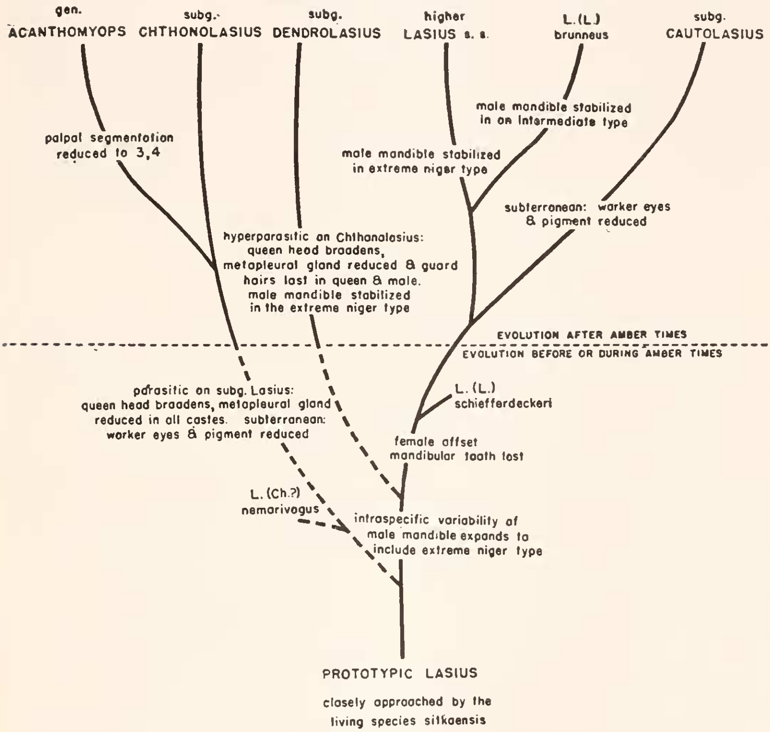

Fig. 2. Phylogeny within *Lasius*. Further explanation in the text.

condition; and *Dendrolasius* and the remainder of living *Lasius s. s.* possess the *niger* type. There is some evidence to indicate that the male morphocline, at least, reflects real sequential evolution. The Baltic amber species *L.* (*L.*) *schiefferdeckeri* Mayr has a highly variable male mandible ranging from *sitkaensis* type to an intermediate type, while the Florissant species *L.* (*L.*) *peritulus* (Ckll.) has the advanced *niger* type.

There is a possibility that *L. sitkaensis* has diverged from the generic prototype by an increase in size and acquisition of standing appendage pilosity. The evidence for this is simply that *L. schiefferdeckeri,* which is intermediate between it and the *niger* complex in the crucial structure of the male mandible, is quite small and lacks standing appendage pilosity. Moreover, both characters appear on other grounds to be specialized conditions which have been developed polyphyletically in several sections of the genus.

If the assumption be made that *sitkaensis* does represent a little-changed derivative of the ancestral population, and that the fossil *schiefferdeckeri* represents the prototype of the higher members of the nominate subgenus (for further evidence see under description of this species) then it becomes possible to thread together the evolutionary history of *Lasius s. s.* in plausible zoogeographic terms. According to the hypothesis which I consider to be the simplest and most consistent with past and modern distributions, the *Lasius* prototype, very similar to the living species *sitkaensis,* at one time ranged over both Eurasia and North America. By Baltic Amber times (Oligocene) the Eurasian segment of this population had evolved into *L. schiefferdeckeri,* a type intermediate between *sitkaensis* and the *niger* complex. At least part of the North American segment, and probably all of it, remained static with respect to this morphocline. By Florissant times (lower to middle Oligocene, see MacGinitie, 1953), the *niger* male mandible type had been stabilized in one or more species, and a species possessing it (*L. peritulus*) had invaded North America. In Europe the *niger* complex was undergoing speciation along the lines already foreshadowed by the variability of the ancestral species *schiefferdeckeri,* and the derivative species were in the process of radiating into several major habitats: *brunneus* was mostly arboreal, *alienus* and *emarginatus* showed southern affinities and favored open, dry situations, and *niger* was more cold-adapted and could penetrate forests in addition to open situations. In North America a different situation prevailed. The old relict species *sitkaensis* was well adapted to the colder forested areas and was not displaced from them by the later *niger* complex invaders. *Alienus*, either the same species as the Florissant *peritulus* or closely related to it, came to occupy the more southern forests. The open habitats were filled with the three species of the *neoniger* complex (*neoniger, crypticus, sitiens*), a specialized group limited to North America and probably derived from an early *niger* complex ancestor. *Niger* itself appears to have reached North America by a later invasion and is today still a relatively uncommon ant limited to the mountains of the western United States.

SOME FINDINGS OF GENERAL THEORETICAL INTEREST

Rate of evolution. Lasius is often cited as a genus with an extremely low rate of evolution. Gustav Mayr (1868) and Wheeler (1914) have stated that the Baltic Amber *L. schiefferdeckeri* Mayr is very little different from the modern siblings *L. niger* (L.) and *L. alienus* (Foerst.) and may be directly ancestral to all the members of the *niger* complex. The present study has included an analysis of this relationship based on a limited collection of amber specimens (see p. 52). *L. schiefferdeckeri* has been shown to differ morphologically from *niger* and other members of the nominate subgenus by about the same amount of difference that separates modern species on the subgenus. As stated previously (under Phylogeny within the Genus) *schiefferdeckeri* appears to be transitional between the hypothetical subgeneric prototype, most closely represented by the living *L. sitkaensis* Pergande, and more advanced species. Moreover, it exhibits variation in the scape index which is transspecific with respect to members of the modern *niger* complex. *L. peritulus* (Ckll.) of the Florissant shales is a true member of the *niger* complex and must be very close to living members such as *L. alienus* (Foerster). Unfortunately, preservation is too poor to allow its specific status to be judged with certainty.

Geographic speciation. There no longer can be any doubt that geographic speciation, as reflected by phenomena in geographic variation, is operative in the better studied groups of higher animals. There is a growing body of evidence to indicate that it occurs generally in all sexually reproducing animals. Indeed, with the exception of germinal polyploidy, which is rare in animals, it is difficult on theoretical grounds to conceive of any scheme of sympatric speciation which is plausible and consistent with our present knowledge of population genetics. By far the simplest process of speciation would seem to be the geographic isolation of populations and their subsequent divergence to potential reproductive isolation.

Species distributions and infraspecific variation patterns in *Lasius* are entirely consistent with the theory of geographic speciation. There is present within the genus all of the different "stages" that would be expected to occur in this process. These can be summarized sequentially as follows.

(1) The geographic variation is barely detectable. Examples: pilosity and body color in *L. sitkaensis,* eye size in *L. umbratus.*

(2) The geographic variation is stronger, producing (in individual characters) conventional subspecies patterns. Examples: pilosity in *L. niger,* male genitalia in *L. niger* and *L. alienus,* pilosity in *L. fuliginosus.*

(3) The geographic variation is very strong, producing differences between terminal populations exceeding those which separate some sympatric species pairs. Examples: appendage length, eye size, and polymorphism in *L. flavus;* habitat preference and nesting habits in *L. alienus.*

(4) Two populations have attained species status by morphological criteria, but still replace one another geographically. Example: *L. emarginatus* and *L. productus.*

(5) Two closely related species are sympatric and tend to replace one another ecologically. Examples: *L. neoniger* and *L. crypticus, L. flavus* and *L. nearcticus.*

The effect of interspecific competition on variation. An interesting situation has been found in *Lasius* which may have an important bearing on the analysis of interspecific hybridization. This is the phenomenon of convergence of related species under the condition of reduced competition to give the false appearance of introgressive hybridization. *Lasius flavus,* for instance, can be separated from *L. nearcticus* by at least eight genetically independent characters where these two species occur together in the eastern United States. In the western United States, where *nearcticus* is rare or absent, *flavus* converges toward it morphologically and assumes as part of an increased variability all but two of the diagnostic *nearcticus* characters. Furthermore, the characters occur together in a variety of combinations. (See under the section on geographic variation in *flavus*.)

A similar but less striking case occurs in *L. niger*. In those parts of North America and eastern Asia where its sister species *alienus* is uncommon, *niger* converges toward and partly overlaps *alienus* in quantity of standing appendage pilosity, the principal character separating the two species. In Europe, where both species are abundant, the two stand far apart in this character, with no sign of overlap. (See under the section on geographic variation in *niger*.)

The importance of this phenomenon is that it illustrates the pronounced effect interspecific competition can have on geographic variation. It also raises a serious objection to the method proposed by Anderson (1951) of using ''concordant'' versus ''discordant'' variation in the detection and evaluation of interspecific hybridization. According to Anderson, the occurrence of discordant (poorly correlated) character variation in a population of plants can be taken as an indication of introgression of genes from a related species. In *Lasius flavus* just the reverse of the condition described by Anderson for plants exists. Where *nearcticus* is in contact with it, *flavus* shows discrete, concordant variation. Where *nearcticus* is absent, the variation is discordant and convergent toward *nearcticus*. Whether a similar condition can exist in plant species remains to be seen, but it remains an important alternative explanation which must be taken into account in future hybridization analyses.

THE SPECIES AND SUBSPECIES CONCEPTS

The treatment of these lesser categories is crucial in a genus with a complex nomenclature such as *Lasius*. My own general views on the subject have already been expressed in a recent paper by W. L. Brown and myself (Wilson and Brown, 1953). We consider that the species represents the only taxonomic unit approaching reality in nature. We agree with E. Mayr (1949a) that the species is only completely objective in terms of local faunas, i.e. where discrete populations co-exist at the same place at the same time. There is a sound evolutionary principle underlying this conclusion. When first brought together in nature any related populations that possess imperfect intrinsic isolating mechanisms will tend to take one or the other of two courses: either they will dispose of all imperfect reproductive barriers that may have arisen during their previous geographic isolation, and completely intergrade to become a single species; or else they will strengthen the reproductive barriers until hybridization is eliminated and thus insure permanent segregation. It is to be expected that intermediate degrees of reproductive isolation would be rare, since interspecific hybrids tend to be sterile and otherwise selectively disadvantageous and therefore an unprofitable venture for the contributing parental populations. There has been some genetic documentation of this crucial step in speciation (see Dobzhansky, 1952, p. 208), and it is borne out as a taxonomic fact that within or between sympatric populations hybridization is in almost every case either complete or else totally absent.

Of course, no such selective force can operate on geographically isolated populations, and it is probable that under this condition every stage of potential reproductive isolation can and does occur with equal frequency. The status of such populations — whether they are conspecific or distinct — can be judged only arbitrarily by comparing their degree of morphological divergence with that existing between sympatric populations of known status.

We have argued, and still argue, that the subspecies, or geographic race, cannot achieve the reality of the sympatric species and must of necessity be arbitrarily defined if it is to be recognized as a category at all. There are several reasons for this, chief among which is the tendency for genetically independent characters to show discordant geographic variation. As a consequence of discordance, the precise limits of any subspecies are set by the character or character combinations chosen by the describer. There is no such thing as a ''natural'' subspecies which can be handily delimited by whatever characters happen to be taxonomically convenient. It is our view that geographic variation should be described in terms of each independent character, and not in terms of geographic segments designated by trinomens. A subspecies pattern fitted with trinomens may be satisfactory so long as only the characters originally employed to describe the pattern are used, but it becomes untenable, and the trinomens artificial and cumbersome, as variation in other characters is studied in more detail.

We have often heard the counterargument that it is the job of the taxonomist to describe variation as completely as possible, and that the designation of trinomens is a desirable part of this process, even if further analysis will eventually necessitate their rearrangement or total dissolution. But what function does the trinomen really perform once it is installed? To answer this question we must first consider the more elementary one, what function does labelling of any sort perform? Few will disagree with the answer that above all things it provides a system of reference for collateral studies in other fields of biology. The mere cataloging of individual specimens will contribute very little to science until it has found application in these studies. It would seem to follow that when a trinomen is used in a study other than a purely taxonomic one, all of its theoretical difficulties will likely become practical deadfalls. In the matter of discordant variation, the physiologist may go astray by expecting variation patterns in physiological characters to show a resemblance to those in the diagnostic morphological characters used by the taxonomist. The ecologist will often encounter variation in habitat preference or food habits which is not indicated by morphological subspecies patterns or which may even run counter to them. The student of speciation may be satisfied to analyze evolution in terms of subspecies units, but he will never accomplish more than a crude description of the process as long as he regards his units as being basic and objective.

Beyond the realm of purely descriptive, ornamental taxonomy, the trinomen is at its worst misleading and at its best superfluous. It may seem at first a convenient kind of shorthand in describing infraspecific variation, but it is far inferior to the direct analysis of genetically independent characters (and subsequent synthesis) with the goal of establishing extent and significance of concordance. With this conclusion as a guiding philosophy I have proceeded in the present revision to synonymize all trinomens, even where they might otherwise have been applied to taxonomically recognizable geographic segments, or ''subspecies'' in the conventional sense. I cannot see that the classification of *Lasius* will suffer in any way from this move; in fact, the limitation of scientific names to the binomen as undertaken here seems to produce the most lucid and practical classification possible within the confines of our present knowledge.

TERMINOLOGY AND MEASUREMENTS

Terminology in the descriptive part of this study follows, as closely as possible, usage prevalent in recent myrmecological literature. To fit the peculiarities of the genus, a few special measurements and indices have been devised. These are presented, along with a few possibly equivocal terms which need precise definition, in the glossary below. All measurements were made with an ocular micrometer fitted in a binocular dissecting microscope at a magnification of 37×. The micrometer span of 100 units covered a distance of exactly 2.97 mm.; measurements made with it were converted to millimeters by means of equivalent ratios. Most measurements were made to the nearest two-tenths of a unit, giving a calculated maximum error of ± 0.006 mm. Duplicate test measurements of pronotal width, head width, and scape length on the same specimens at an interval of several months concurred precisely in the majority of cases, differed by 0.2 unit in less than one-third of the cases, and hardly ever differed by as much as 0.4 unit. It is therefore safe to say that the measurements of these three most important dimensions have been very consistent in the course of the study, insuring accurate ratios and indices, and that they are probably precise to within a margin of ± 0.01 mm. or less. Other, grosser measurements, such as the head width and thorax width of the queen, probably have a somewhat larger margin, but in no case does it exceed ± 1 unit, or ± 0.03 mm.

Alitrunk. The entire median tagma of the body, consisting of the fused true thorax and propodeum.

Allometry. A size relationship betwen two structures or between a structure and the entire body, such that a dimension of one is a simple power function of a dimension of the other. In the present study the term is used in its more limited sense, implying disproportionate growth between two organs. An understanding and use of the concept of allometry is essential in the taxonomy of a genus such as *Lasius,* where absolute measurements or indices are of little value unless expressed as a function of total size. The conventional method of representing allometry is by means of a double logarithmic graph, which con-

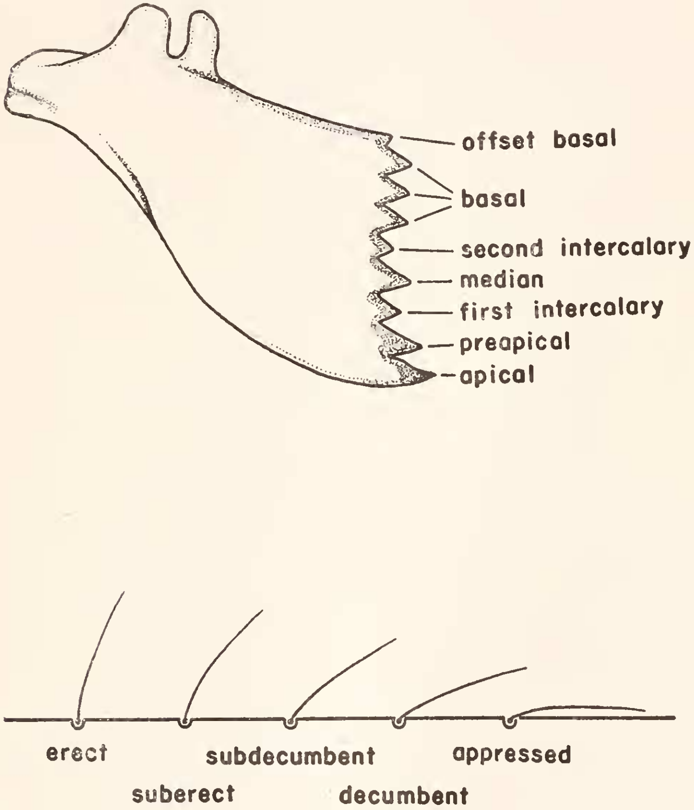

Fig. 3. *Above,* mandible of *L. sitkaensis,* showing the generalized formicine dentition and attendant nomenclature used in the present study. The offset basal tooth is a primitive character in the genus. *Below,* the nomenclature used in the present study to describe inclination of pilosity with respect to the cuticular surface.

verts the exponential curve into a straight line. However, size variation in *Lasius* is not sufficiently great to allow the expression of a curvilinear form and so all the graphs represented herein are simple arithmetical ones. Data are plotted individually in scatter diagrams, and the patterns they form are termed "regression zones."

Allopatric. Applied to populations occupying mutually exclusive ranges during the breeding season.

Cephalic index (CI). Head width × 100/head length.

Cryptic species. A species which so closely resembles other species that it is difficult or impossible to detect by the use of conventional taxonomic characters.

Dentition. A survey of the Formicinae made in connection with this revision has revealed the presence of a widespread elementary pattern in mandibular dentition. This pattern, exemplified by *Lasius,* has been provided with a special terminology illustrated in Figure 3. An offset basal tooth is a primitive character in *Lasius* and is present in only a few species of the genus.

Eye length (EL). The maximum measurable length of the eye.

Eye width (EW). The maximum width of the eye measured at a right angle to the long axis.

Head length (HL). The length of the head, held in perfect full face, measured from the midpoint of the anterior border of the median clypeal lobe to the midpoint of the occipital border.

Head width (HW). Worker and queen: the maximum width of the head held in perfect full face and excluding the eyes. If the eyes extend beyond the lateral borders of the head in this position, the measurement is taken across whatever part of the lateral borders are left exposed. *Male:* the maximum width of the head across and including the eyes.

Maxillary palpal length (ML). The maximum length of the terminal segment of the maxillary palp, measured from the distalmost part of the rim of the penultimate segment to the tip of the terminal segment.

Nidotype. A specimen from the same nest as the holotype or lectotype.

Paramere length. The length as defined by Clausen (1938), measured exactly parallel to the long axis from the level of the distalmost part of the basiparamere to the level of the tip of the paramere.

Perfect full face. The head as seen in frontal view when held so as to attain maximum length and with the anterior border of the median clypeal lobe and occipital border horizontally aligned.

Pilosity. The longer, stouter hairs, or setae, which are outstanding above the shorter, usually finer hairs which constitute the pubescence. A special terminology, adopted from an unpublished doctoral thesis by F. G. Werner (Harvard University, 1950) and illustrated in Figure 3, has been employed herein to describe the angle of inclination from the cuticular surface.

Pronotal width (*PW*). The maximum width of the pronotum measured from directly above and at a right angle to the long axis of the alitrunk.

Propodeum. The equivalent of the "epinotum" of most earlier myrmecological work, i.e. the first segment of the abdomen which is, in higher Hymenoptera, fused to the thorax to form with it a single structure, the alitrunk.

Pubescence. The shorter, usually finer hairs underlying the pilosity (see definition above). The terminology of Figure 3 relating to angle of inclination applies to pubescence as well as to pilosity.

Scape index (*SI*). Scape length × 100/head width.

Scape length (*SL*). The maximum measurable length of the scape exclusive of the basalmost "neck".

Seta count. The number of standing hairs (see definition below) which can be seen extending beyond the outline of the following appendage surfaces: the anterior scape surface viewed in line with the plane of funicular flexion, and the outer surface of the fore tibia viewed in line with the plane of tibial flexion.

Standing hair. A hair which is subdecumbent, suberect, or erect, i.e., forming an angle with the cuticular surface of 45° or more.

Subgenital plate. In the male, the terminal sternite (IX) just underlying the genitalia.

Sympatric. Applied to populations the breeding ranges of which overlap, at least in part.

Key to the Species of Lasius, Based Principally on the Workers: Nearctic

1. Maximum worker eye length 0.20 × the head width or more.........2
   Maximum worker eye length 0.17 × the head width or less..........7

2. In a given nest series all larger *workers* (PW 0.57 mm. or more) and most smaller workers with one or more offset teeth at the basal angle of the mandible; *male* mandible with a narrow preapical cleft setting off a narrow, acute apical tooth, and with a well defined basal angle (Pl. 1) ....*sitkaensis* Pergande
   Workers of all sizes with the posterior basal tooth aligned with the adjacent teeth of the masticatory border; *male* mandible lacking a narrow preapical cleft and well-defined basal angle, the masticatory border curving gradually into the basal border (Pl. 1) 3

3. Maximum eye length usually less than 0.25 × the head width and never more; color always yellowish brown; scapes always lacking standing hairs (southwestern U. S. and Mexico) ....*sitiens* Wilson
   Maximum eye length exceeding 0.25 × the head width, even if only slightly; color occasionally yellowish brown, but then the scapes have standing hairs 4

4. In one or both mandibles of a majority of the nest series, either the penultimate basal tooth is markedly reduced in size relative to the two flanking teeth, or the gap between the penultimate and terminal basal teeth tends to be larger in area than the terminal basal tooth and variable in shape; when viewed with the mandibles opened and the head held in perfect full face (at maximum head length and with the occipital and anterior clypeal borders horizontally aligned), the anterior border of the median clypeal lobe is angulate, i.e. formed of two straight sides meeting at the midline to form an obtuse, usually pointed angle (Pl. 1) 5
   In all of the workers of a nest series, with rare exceptions, the penultimate and terminal basal teeth are subequal in size, and the gap between them has about the same area as the terminal tooth and is constant in shape; when viewed with the mandibles opened and the head held in perfect full face, the anterior border of the median clypeal lobe describes an even, broad parabolic curve, with the sides at least feebly convex and only occasionally meeting in a point at the midline (Pl. 1) 6

5. The scapes and tibiae of all workers except nanitics (PW less than 0.40 mm.) bearing standing hairs; body color light brown to medium brown, very rarely dark brown ....*neoniger* Emery
   The scapes and tibiae lacking standing hairs and usually without hairs

of any inclination (but pubescence still abundant); color typically dark brown ....*crypticus* Wilson

6. Within the size range PW 0.53–0.70 mm., scapes and tibiae bearing few or no standing hairs, the seta count (see under Terminology and Measurements) always less than 20 and usually less than 10 (refer to the PW-seta count regression zones of Fig. 6) ....*alienus* (Foerster)

Within the above size range, the scapes and tibiae bearing numerous standing hairs, the seta count usually greater than 10 (western U. S. only) ....*niger* (Linnaeus)

7. Dorsal crest of the worker petiole seen in frontal view strongly convex and non-emarginate ....*humilis* Wheeler

Dorsal crest of the worker petiole at most feebly convex and often emarginate 8

8. Eyes with less than 35 ommatidia 9

Eyes with 35 or more ommatidia 11

9. Outer surfaces of each tibia with numerous standing hairs prominent above the ground pubescence (western U. S.) ....*fallax* Wilson

Outer surfaces of each tibia with at most one or two standing hairs..10

10. Terminal segment of the maxillary palp longer than the penultimate segment in at least a majority of the workers of the nest series (eastern North America to Wyoming) ....*nearcticus* Wheeler

Terminal segment of the maxillary palp in all of the workers of the nest series at most as long as the penultimate segment (Nova Scotia to California) ....*flavus* (Fabricius)

11. At least a broad longitudinal median strip of the second gastric tergite, exclusive of the extreme posterior portion, almost completely devoid of pubescence of any kind and with only a few widely scattered standing hairs, its cuticular surface extremely smooth and shining at low magnifications (eastern U. S.) ....*speculiventris* Emery

Central area of second gastric tergite covered by abundant pubescence and standing hairs, its surface feebly shining to subopaque at low magnifications 12

12. Longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, not exceeding in length 0.50 × the maximum width of the hind tibia at its midlength.................
.....................................*umbratus* (Nylander)

Longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, at least 0.60 × as long as the maximum width of the hind tibia at its midlength 13

13. *Worker:* body color brownish yellow; lateral tibial surfaces completely lacking standing hairs; longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, often as long as the maximum width of the hind tibia at midlength or longer;

pubescence of gastric tergites dense, often lending a greyish overcast to the cuticle under low magnifications; *queen* small, HW 1.02–1.17 mm. (eastern North America) ....*minutus* Emery

Worker: body color clear yellow; lateral tibial surfaces often with standing hairs; longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, never exceeding 0.80 × the maximum width of the hind tibia at midlength; pubescence of gastric tergites lighter, rarely dense enough to lend a greyish overcast to the cuticle; *queen* larger, HW never less than 1.30 mm. 14

14. Pilosity of posterior half of first gastric tergite, exclusive of the extreme posterior strip, at least in part decumbent-subdecumbent; standing hairs sparse or absent on the lateral tibial surfaces (maritime Canada to Arizona) ....*subumbratus* Viereck

Pilosity of posterior half of first gastric tergite, exclusive of the extreme posterior strip, almost entirely suberect-erect; standing hairs often abundant on the lateral tibial surfaces (Pacific Coast to Idaho) ....*vestitus* Wheeler

Key to the Species of Lasius, Based Principally on the Workers: Palaearctic[1]

1. Maximum worker eye length 0.20 × the head width or more 2

Maximum worker eye length 0.17 × the head width or less 6

2. In *workers* with HW 0.79–1.21 mm., the SI ranges 82–94 and is usually 91 or less (see Fig. 5); alitrunk and petiole homogeneous light reddish brown, contrasting against the dark brown gaster; scapes and tibiae lacking standing hairs and usually hairs of any inclination; body pilosity sparse, the curving portion of the occipital corners viewed in full face typically devoid of hairs, rarely with one or two; *males* large, HW 1.04–1.10 mm. in three nest series examined; mandible with a shallow cleft separating the anterior and posterior halves of the masticatory border ....*brunneus* (Latreille)

In *workers* with HW 0.79–1.21 mm., the SI is 95 or more; body coloration variable, rarely exactly as in *brunneus;* scapes and tibiae often with standing hairs; curving portion of occipital corners usually with two or more standing hairs; *males* with HW rarely greater than 1.04 mm., usually less than 1.00 mm.; mandible lacking a clearcut cleft on the masticatory border 3

3. In workers with HW 0.86–1.12 mm., the SI ranges 112–124; if outside this HW range, then the SI should fit an extrapolation of the SI-HW regression zone shown in Figure 5 (Japan) ....*productus* Wilson

Within the same worker HW range, SI does not exceed 109 and is usually

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[1] Excludes *L. buccatus* Stärcke and *L. teranishii* Wheeler, members of the subgenus *Dendrolasius* known only from sexual forms; see key to the queens.

much less 4

4. The worker possessing at least one and usually both of the two following characters: (1) alitrunk and petiole yellowish red, contrasting with the medium to dark reddish brown head and gaster (body tending to concolorous reddish brown in the Balkans area; see under geographic variation of this species); (2) scape with numerous preponderantly subdecumbent hairs. In addition, SI is 103–109 within a HW range of 0.61–1.10 mm. (Europe) ....*emarginatus* (Olivier)

Worker body concolorous reddish brown to blackish brown; within the range of *emarginatus* in Europe, the scape either lacks standing hairs or these are preponderantly suberect-erect. In all populations of *alienus* except that in the Balkans area, and in all of *niger* except those in North Africa, the Balearics, the Atlantic Islands, and eastern Asia, the SI is 95–103 within a HW range of 0.61–1.10 mm. 5

5. In workers with PW 0.53–0.70 mm., scapes and tibiae with few or no standing hairs, the seta count (see under Terminology and Measurements) always less than 20 and usually less than 10.*alienus* (Foerster)

Within the above size range, European workers usually possess seta counts of 20 or more; Asiatic workers often range below this and in some cases may be distinguishable only by comparing intranidal trends with the regression zones of Figure 6......*niger* (Linnaeus)

6. *Worker* body color jet black; the scutum of the *queen* seen in perfect side view overhangs the pronotum and claims the entire anterior thoracic convexity 7

Worker body color yellow to yellowish brown; the scutum of the queen does not overhang the pronotum but shares with it the anterior thoracic convexity 9

7. Antennal scapes of the worker flattened to the extent that for most of their length the minimum measureable width at any point is less than half the maximum measurable width at that point; the *queen* is an extreme "beta" form, with greatly flattened scapes, femora, tibiae, and metatarsi (Japan and Korea) ....*spathepus* Wheeler

Antennal scapes of the worker short-elliptical in cross-section, so that for most of their length the minimum width at any point is 0.8 × the maximum width at that point or more; the *queen* is an "alpha" form, with normal appendages, the scape short-elliptical in cross-section 8

8. *Queen* with many body and appendage hairs curved at the tip or sinuate, those on the appendages often curving back to touch the cuticular surface again; body pubescence sparse or absent, the cuticular surface smooth and shining; *worker* (tentatively associated) with the standing hairs of the second and third gastric tergites (exclusive of

the extreme posterior strips) reaching a maximum length of 0.10–0.12 mm. and as long as the standing hairs on the pronotum or longer; in side view the petiolar crest thin and sharp (Pl. 2, fig. 8) (Japan and Korea) ....*crispus* Wilson

Queen with few or no hairs curved at the tip or sinuate; body covered with abundant appressed pubescence which at least partly obscures the shining cuticular surface; *worker* with the standing hairs of the second and third gastric segments (exclusive of the extreme posterior strips) never as long as 0.10 mm. and rarely exceeding 0.08 mm., usually shorter than the standing hairs of the pronotum; the petiolar crest in side view thicker and blunter (Pl. 2, fig. 7) (England to Japan) ....*fuliginosus* (Latreille)

9. Dorsal crest of the worker petiole seen in frontal view strongly convex and never emarginate 10

Dorsal crest of the worker petiole at the most feebly convex and often emarginate 11

10. Eyes of *worker* set in shallow but distinct circumocular depressions; pilosity of first gastric tergite predominantly decumbent; PW not exceeding 0.63 mm.; *queen* exceedingly small, HW 0.76–0.78 mm..... ....*carniolicus* Mayr

Eyes of *worker* not set in depressions; pilosity of first gastric tergite predominantly subdecumbent-erect; PW of three workers measured 0.88–0.93 mm.; *queen* exceptionally large, HW of single specimen measured 1.99 mm. (known only from the Himalayas) ....*crinitus* (F. Smith)

11. Worker eyes with less than 30 ommatidia (if the nest series splits on this couplet, go to 12) 12

Worker eyes with more than 30 ommatidia 13

12. Scapes and tibiae of worker with numerous standing hairs prominent above the ground pubescence (eastern Asia) ....*talpa* Wilson

Worker scapes and tibiae with few or no standing hairs (England to Japan) ....*flavus* (Fabricius) in part

13. In both the worker and queen, the dorsal border of the petiole in frontal view narrow and deeply emarginate, the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination at least as great as the width of the emargination measured at the level of the middle of the depth measurement ....*bicornis* (Foerster)

Dorsal border of the petiole with never more than a right-angular emargination 14

14. Either the genal margins of the *worker* seen in full face with standing hairs prominent above the ground pubescence; or else the longest hairs of the posterior half of the first gastric tergite (exclusive of

the extreme posterior strip) are distinctly less than half as long as the maximum width of the hind tibia at its midlength. In the *queen* the head width is about the same as the width of the thorax just anterior to the tegulae or greater ....
umbratus (Nylander) or *rabaudi* (Bondroit), (see key to queens).

Genal margins of *worker* seen in full face lacking standing hairs; the longest hairs of the posterior half of the first gastric tergite (exclusive of the extreme posterior strip) at least half as long as the maximum width of the hind tibia at its midlength. In the *queen* the head width is much less than the width of the thorax just anterior to the tegulae 15

15\. (A species known from only one nest series from the Himalayas.) Terminal maxillary palp segment of worker slightly longer than the penultimate segment; the segments as a whole longer (see under diagnosis of this species) ....*alienoflavus* Bingham

(A widespread and abundant Holarctic species.) Terminal maxillary palp segment of worker at most as long as the penultimate ....
....................................*flavus* (Fabricius), in part

Key to the Queens of Lasius[1]

1\. Metapleural gland opening provided with conspicuous guard hairs; in side view the scutum does not overhang the pronotum but shares with it the anterior thoracic convexity 2

Metapleural gland opening lacking guard hairs; in side view the scutum overhangs the pronotum and claims all of the anterior thoracic convexity 22

2\. HW distinctly less than the width of the thorax just anterior to the tegulae 3

HW about the same as or greater than the width of the thorax just anterior to the tegulae 13

3\. Length of terminal segment of maxillary palp exceeding 0.1 × the HW, even if only slightly 4

Length of terminal segment of maxillary palp less than 0.1 × the HW, even if by only a slight amount 10

4\. When viewed with mandibles opened and the head held in perfect full face (at maximum head length and with the occipital and anterior clypeal borders horizontally aligned), the median third of the anterior border of the median clypeal lobe is flat or emarginate; all the queens of a nest series with at least one and often two or three offset teeth present on the basal angle and along the basal border of the mandible (North America) ....*sitkaensis* Pergande

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[1] Excluding the rare Himalayan species *alienoflavus* (see key to workers).

When viewed as above, the median third of the anterior border of the median clypeal lobe convex or angulate, never flat or emarginate; the posterior basal tooth, with rare exceptions, always aligned with the adjacent teeth of the masticatory border; when it is offset, this condition occurs in a minority of the individuals of the nest series and usually only on one mandible in any individual, and secondary offset teeth are never present on the basal border 5

5. When viewed with the mandibles opened and the head held in perfect full face, the anterior border of the median clypeal lobe is angulate, with two straight or very feebly convex sides meeting in a blunt point at the midline; in a large part of any nest series the penultimate basal tooth is distinctly reduced in size relative to the two flanking teeth (North American species only) 6

When viewed as above, the anterior border of the median clypeal lobe is broadly and evenly rounded; with rare exceptions the penultimate basal tooth is about the same size as the two flanking teeth 7

6. Scapes and tibiae with numerous standing hairs ....*neoniger* Emery

Scapes and tibiae lacking standing hairs ....*crypticus* Wilson and *sitiens* Wilson

7. Length of terminal segment of maxillary palp 0.32–0.34 mm. in the several series measured (Japan) ....*productus* Wilson

Length of terminal segment of maxillary palp not exceeding 0.26 mm...8

8. Scape with numerous standing hairs ....*niger* (Linnaeus)

Scape with few or no standing hairs, although decumbent hairs may be numerous 9

9. Scape with numerous decumbent hairs outstanding above the pubescence ....*emarginatus* (Olivier)

Scape with few or no decumbent hairs outstanding above the pubescence ....*alienus* (Foerster) and *brunneus* (Latreille)

10. Scape with numerous standing hairs (eastern Asia) ......*talpa* Wilson

Scape with few or no standing hairs 11

11. Tibiae with numerous standing hairs (western U.S.).....*fallax* Wilson

Tibiae with few or no standing hairs 12

12. Terminal segment of maxillary palp usually longer than the penultimate (see diagnosis) (eastern North America to Wyoming) ....*nearcticus* Wheeler

Terminal segment not exceeding in length the penultimate segment (Holarctic) ....*flavus* (Fabricius)

13. HW 0.76–0.78 mm.; petiole in side view thick, resembling an inverted U (Eurasia) ....*carniolicus* Mayr

HW exceeding 1.00 mm.; petiole in side view thinner, with a narrow dorsal crest 14

14. Alitrunk and gaster covered with extremely long, fine, predominantly appressed hairs; HW of single specimen measured 1.99 mm. (Himalayas) .... *crinitus* (F. Smith)
Pilosity of alitrunk and gaster otherwise; HW never exceeding 1.75 mm. 15

15. The dorsal border of the petiole in frontal view narrow and deeply emarginate, the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination at least as great as the width of the emargination measured at the level of the middle of the depth measurement (Eurasia) .....*bicornis* (Foerster)
Dorsal border of the petiole with never more than a right-angular emargination 16

16. HW not exceeding 1.17 mm. 17
HW at least 1.40 mm. 18

17. First gastric tergite densely covered with coarse standing hairs, the longest of which exceed in length the maximum width of the hind tibia at its midlength (eastern North America) ....*minutus* Emery
First gastric tergite with relatively sparse, fine hairs, the longest of which do not exceed in length 0.8 × the maximum width of the hind tibia at its midlength (southwestern U. S.) ....*humilis* Wheeler

18. The longest hairs of the first gastric tergite exclusive of the extreme posterior strip not exceeding in length 0.5 × the maximum width of the hind tibia at its midlength 19
The longest hairs of the first gastric tergite, exclusive of the extreme posterior strip, about as long as the maximum width of the hind tibia at its midlength...21

19. Dorsal surfaces of second and third gastric tergites completely devoid of pubescence and strongly shining (eastern U.S.)..*speculiventris* Emery
Dorsal surfaces of second and third gastric tergites covered by appressed pubescence which often partly obscures the shining cuticular surface 20

20. Scapes conspicuously flattened, the minimum width at midlength not exceeding 0.10 mm. (Fig. 15) (Eurasia) ....*rabaudi* (Bondroit)
Scapes short-elliptical in cross-section, the minimum width at midlength not less than 0.11 mm. (Holarctic) ....*umbratus* (Nylander)

21. Pilosity of anterior gastric tergites predominantly erect.*vestitus* Wheeler
Pilosity of anterior gastric tergites predominantly decumbent-subdecumbent ....*subumbratus* Viereck

22. A "beta" form, with conspicuously flattened scapes, femora, tibiae, and metatarsi; thorax completely lacking hairs of any kind 23
An "alpha" form, showing no conspicuous flattening of the appendages; thorax with abundant hairs 24

23. Head about as broad as long; petiolar scale symmetrical in side view, with both the anterior and posterior faces gently convex ....*teranishii* Wheeler

Head much broader than long, anterior border of petiolar scale in side view angulate, being parallel with the posterior border up to the level of the petiolar spiracle but then bending abruptly back to form an oblique face up to the dorsal crest ....*spathepus* Wheeler

24. Many of the body and appendage hairs curved at the tip or sinuate, those on the appendages often curving back to touch the cuticular surface again; body pubescence sparse or absent, the cuticular surface smooth and shining ....*crispus* Wilson

Few or no hairs curved at the tip or sinuate; body covered with appressed pubescence which at least partly obscures the cuticular surface 25

25. A sharp median carina runs from the frontal triangle to a small shallow pit in the center of the clypeus; CI about 97 ......*buccatus* Stärcke

Median clypeal carina weakly developed and running most of the length of the clypeus, not ending in a central pit; CI as least 100 ....*fuliginosus* (Latreille)

Key to the Males of Lasius[1]

1. Metapleural gland opening provided with guard hairs 2

Metapleural gland opening lacking guard hairs 12

2. Mandible lacking a preapical cleft, at the most the masticatory border feebly impressed in the middle; basal angle of mandible always broadly rounded, the masticatory border curving gradually into the basal border 3

Mandible with a distinct preapical cleft (occasionally lacking in smaller individuals with HW less than about 1.00 mm.); basal angle often distinctly marked and clearly separating the masticatory and basal borders 6

3. SI exceeding 100 ....*productus* Wilson

SI less than 80 4

4. Standing hairs common on the scape ....*niger* (Linnaeus) and *neoniger* Emery

Standing hairs rare or absent on the scape 5

5. Subgenital plate arc-shaped, with a deeply concave posterior border sweeping back to the prominent posterolateral flanges, and with the anterior border correspondingly convex (Europe) ....*emarginatus* (Olivier)

Subgenital plate subquadrate, the posterior border flat or weakly con-

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[1] The males of the following species are unknown or were not available during the present study: *alienoflavus, bicornis, crinitus, humilis, teranishii,* and *vestitus.*

cave and the posterolateral flanges weakly developed or absent ....*alienus* (Foerster), *crypticus* Wilson, and *sitiens* Wilson

6. HW exceeding 1.00 mm.; basal angle of the mandible indistinct, the masticatory border merging gradually into the basal border (Eurasia) ....*brunneus* (Latreille)

Either HW less than 1.00 mm., or else the basal angle of the mandible is distinct and clearly demarcates the masticatory and basal borders...7

7. HW distinctly less than the width of the thorax just anterior to the tegulae 8

HW at least as great as the width of the thorax just anterior to the tegulae (subg. *Chthonolasius*) 9

8. ML exceeding 0.10 mm. ....*sitkaensis* Pergande

ML less than 0.08 mm. ....subg. *Cautolasius* (*flavus*, *nearcticus*, *talpa*, *fallax*)

9. At least a broad longitudinal median strip of the second gastric tergite completely devoid of pubescence, its cuticular surface shining (eastern U.S.) ....*speculiventris* Emery

All of second gastric tergite covered with abundant pubescence which at least partly obscures the cuticular surface 10

10. Petiole in side view thick, with a broadly rounded dorsal crest; standing hairs abundant around the entire cephalic margin (seen in full face) posterior to the eyes (Eurasia) ....*carniolicus* Mayr

Petiole in side view thin, with an acute dorsal crest; much of the cephalic margin posterior to the eyes bare of pilosity 11

11. Longest hairs of the first gastric tergite exceeding 1.5 × the maximum width of the hind tibia at midlength; longest hairs of the posterior two-thirds of the clypeus exceeding 0.16 × the HW (eastern North America) ....*minutus* Emery

Longest hairs of the first gastric tergite not exceeding 1.1 × the maximum width of the hind tibia at midlength; longest hairs of the posterior two-thirds of the clypeus not exceeding 0.10 × the HW 12

12. Maximum length of the hairs of the first gastric tergite 0.9–1.1 × the maximum width of the hind tibia at its midlength (Nova Scotia to Arizona) ....*subumbratus* Viereck

Maximum length of the hairs of the first gastric tergite not exceeding 0.7 × the maximum width of the hind tibia at its midlength ....*umbratus* (Nylander) and *rabaudi* (Bondroit)

13. Mandibles with seven well developed teeth including the apical; in frontal view the genae strongly convex, the head about as wide directly in front of the eyes as directly behind ......*buccatus* Stärcke

Masticatory border of mandible smooth, or at most with several small, irregular denticulae; in frontal view the genae feebly convex, the head directly in front of the eyes at the most 0.9 × as wide as directly behind the eyes 14

14\. In side view the posterior margin of the petiolar scale is gently convex from the level of the posterior foramen to the dorsal crest, while the anterior border is parallel with it up to the petiolar spiracle and then turns abruptly posteriorly to produce a second face up to the crest (Japan and Korea) .... *spathepus* Wheeler

The petiolar scale in side view symmetrical, the posterior border showing the same degree of convexity as the anterior 15

15\. The petiole in side view with a narrow, sharp crest (Japan and Korea) .... *crispus* Wilson

The petiole in profile with a thick, convex crest (England to Japan) .... *fuliginosus* (Latreille)

SYSTEMATIC TREATMENT BY SPECIES

Lasius sitkaensis Pergande

(Subg. *Lasius*)

Lasius niger sitkaensis Pergande, 1900, Proc. Wash. Acad. Sci., **2:** 519–520, worker; original description. Type locality; Sitka, Alaska.

Lasius niger var. *sitkaensis,* Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston, **52:** 524, *part.*

Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 420, *part.* [*nec* Emery 1893].

DIAGNOSIS. *Worker* (1) All medium-sized and larger individuals (PW 0.57 mm. or greater) as well as many nanitics, with an "offset" tooth at the basal angle of the mandible, conspicuously smaller than the adjacent teeth of the masticatory border and often directed more posteriorly; this tooth may be succeeded posteriorly by one or (rarely) two serially arranged, smaller teeth on the basal border (Pl. I, Fig. 1). The entire basal angle, teeth included, tends to be rounded, not sharply angular as in the higher members of the subgenus.

(2) Subdecumbent to erect hairs common on scapes and fore tibiae of individuals with PW 0.57 mm. or greater. Size averaging larger than other members of the subgenus (see under further description below).

Queen. (1) Possessing an offset basal tooth similar to the worker's; secondary teeth on basal border very frequent.

(2) Clypeus lacking a perceptible carina; middle third of

the anterior border of the median lobe straight or shallowly concave.

(3) Scapes and fore tibiae with abundant subdecumbent to erect hairs.

Male. (1) Sclerotized setiferous area of the posterior margin of the subgenital plate (sternite IX) unilobed to bilobed, with all intermediate conditions, but never projecting beyond the unsclerotized rim, with the result that the entire posterior border within the lateral flanges is straight or nearly straight.

(2) Mandible with a well marked basal angle separating the masticatory and basal borders; a distinct apical tooth is set off by a deep, relatively narrow preapical cleft; the masticatory border is straight and frequently armed with irregular denticles which are best developed apicad and obsolescent basad, rarely extending past the midpoint of the border (Pl. 1, Fig. 4).

LECTOTYPE. By present selection, a worker in the MCZ labelled "Sitka, Alaska; June-99; T. Kincaid Coll. 80." PW 0.85 mm., HW 1.26 mm., HL 1.28 mm., SL 1.15 mm., SI 92, ML (right) 0.22 mm., EL 0.28 mm., seta count 40. Left mandible, viewed closed and *in situ,* with a single offset tooth at the basal angle; basal angle of right mandible not visible. Anterior border of median clypeal lobe broadly and evenly rounded, very slightly flattened medially; no carina visible. All of body and appendages light brown, appendages a shade lighter than body and approaching yellowish brown. Syntopotypes in MCZ, AMNH, and USNM.

FURTHER DESCRIPTION. *Worker.* In a sample of 266, with no more than 2 per nest series, PW range 0.40-0.89 mm., mean with standard error 0.650 ± 0.006 mm., standard deviation 0.084 mm. SI in 25 nest series measured (encompassing most of the size variation) formed an allometric regression zone intermediate between *brunneus* and *niger,* closer to *niger* but with the same slope as *brunneus* (*q.v.*), so that above PW of about 1.05 mm., *sitkaensis* diverged strongly from *niger* and showed little individual overlap with that species (see Fig. 5). Maxillary palp segments IV, V, and VI subequal; segment VI (ML) averaging about 1.03 × as long as the EW. The basal mandibular tooth very variable in nanitic workers; in series from incipient colonies, where the worker PW averages 0.5 mm. or less, the mandibles vary from the "*niger* form", in which there is no offset basal tooth and the basal border runs straight to the edge of the first major tooth of the masticatory border, through a series in which the offset tooth appears as a variously developed convexity on the basal border, to the typical "*sitkaensis* form" already described. In incipient colonies, the majority of workers show some development of the offset basal tooth, while in larger colonies the frequency of the tooth approaches 100 per cent, and secondary teeth on the basal border are common. The masticatory teeth follow the general *Lasius* pattern well (Fig. 3), but the basal segment is more variable than in other members of the subgenus. There are typically three, and rarely four, basal teeth exclusive of and anterior to the offset tooth. Occasionally the second intercalary tooth is missing, or there is a secondary intercalary tooth developed between two of the basal teeth, or one of the basal teeth is bifurcate.

The clypeus appears evenly convex in full face and feebly emarginate when viewed antero-obliquely. Head and body broader and more massive relative to total length than in all other *Lasius s. s.* excepting *brunneus;* this difference is subject to allometric modification, since *sitkaensis* nanitics are little different in body form from medium-sized *niger* and *alienus,* while very large *niger* and *alienus* resemble closely, but not completely, medium-sized *sitkaensis.* Posterior margin of head concave in full face view. Promesonotal suture deeply impressed in medium-sized workers; this was a character proposed by Creighton (1950) to separate "*niger neoniger*" from "*alienus americanus*", but it can be used only with qualification, since it is strongly allometric and includes some interspecific overlap. Dorsal margin of petiole in frontal view flat to strongly convex, rarely emarginate.

Entire body, including occipital margin and gastric tergites, covered with abundant standing hairs. Standing hairs about as abundant on appendages as in *niger;* i.e. in the majority of nest series, workers with pronotal width around 0.24 mm. have seta counts between 20 and 40. A higher percentage of the hairs are subdecumbent than in *niger,* where nearly all are typically suberect-erect. The seta count is strongly allometric and is usually less than 10 in nanitics. Superimposed on the allometric variation is a genetic one; the regression zone varies internidally. At one extreme (by nest series), nanitics with PW of 0.5 mm. or less give seta counts between 10 and 20, while workers with PW of 0.7 mm. or more often exceed 40. At the opposite extreme, nanitics give seta counts of 0 and larger workers usually fall below 20. Body pubescence well developed, tending to be denser on the genae and sparser on the gastric tergites than in *niger,* so that even to the naked eye the genae are notably more opaque and the gaster shinier than in that species.

Color usually overall light brown, but ranging from yellowish brown (rare) to dark brown (common).

Queen. HW 1.76-1.99 mm. Mandibular dentition varying as in the worker, except that the offset basal tooth is only rarely reduced to a mere convexity, and no example has been found in which it is entirely missing. In a majority of cases the anterior border of the median clypeal lobe (seen in perfect full face) is emarginate to some degree; it is never convex as in other *Lasius.* The head is more massive relative to the thorax and the occipital zone is broader relative to the anterior part of the head than in other members of the subgenus, but this is probably in part a simple function of the larger total size attained. Standing pilosity with same density as in the worker, showing similar allometric and genetic variation. Hairs of scape shorter and finer than in *L. niger,* the standing hairs seen dorsally and perpendicular to the plane of articulation seldom longer than one-third the greatest width of the scape. Color and pubescence as in the worker. Wings overall infuscate, rather faintly in the distal two-thirds and darkest in the costal cell and area proximal to the discoidal cell.

Male. HW 0.81-0.95 mm. Mandible never differing substantially from the main diagnostic features previously stated, i.e. always possessing a sharp preapical cleft and a well defined basal angle. The masticatory denticles, on the other hand, are highly variable. Usually two denticles are present, but there may be three or none, and they are always irregular in size and placement. In one exceptional series (Rico, Dolores Co., Colo.; MCZ) denticles were developed on the basal angle.

Clypeus lacking a median carina, the anterior border of its median lobe broadly rounded. Dorsal margin of the petiole variably convex, occasionally flat or feebly emarginate.

That part of the posterior margin of the subgenital plate inclosed in the posterolateral flanges always straight to feebly convex in the many specimens dissected; the sclerotized posterior setiferous lobes do not push out beyond the transparent posterior margin of the plate to form a conspicuous convexity as in many other members of the subgenus. The degree of lobing within the setiferous area varies greatly within single nest series. One nest series studied (Morris, Ramsey Co., N. Dak.; P. B. Kannowski leg.; G. C. Wheeler Coll.) exhibited almost all of the maximum variation for the species, the posterior setiferous margin ranging from straight to bilobed. Another series from the same locality showed the alternative condition, a single median lobe. Paramere broadly finger-shaped, typically narrower than in related species, its width at midlength about ⅕ to 1/3 its length. Paramere length relative to head width similar to the European population of *L. niger* (Fig. 7); HW/paramere length ratios measured in 16 nest series varied between 0.95/0.33 and 0.82/0.37 (in mm.); absolute paramere length ranged 0.28-0.37 mm. Volsella typical for genus. Pygostyle broadly finger-shaped, the tip about as wide as the membranous base.

Appendages with dense pubescence but with standing hairs much sparser than in worker and predominantly subdecumbent-suberect. Seta count seldom if ever exceeding 10, usually 5 or less, and often 0. Body hairs notably sparser than in the worker and queen, but still abundant over the alitrunk and entire surfaces of the gastric tergites. Body color medium brown to black, the appendages light to dark brown; both overall lighter than in other members of the subgenus. In lighter specimens the head is typically darker than the alitrunk and the alitrunk darker than the gaster and appendages.

GEOGRAPHIC VARIATION. *Sitkaensis* is surprisingly uniform over its entire range, despite the occasional occurrence of striking variation within single nest series or local populations. A single weak unilateral trend is found in the northwestern segment of the range, including British Columbia and Alaska. In this area there have been encountered a significantly higher percentage of series with sparse appendage pilosity. Partly correlated with this character is a darkening of color. Unfortunately both characters are highly subjective, and intermediate conditions are very difficult to judge. I have attempted to cope with this situation by placing each series in one or the other of two classes for each character: extreme depilation (PW 0.5 mm. with seta count 0, PW 0.8 mm. with seta count less than 20) is marked *h* and dark brown coloration is marked *l*, while the opposing extreme conditions and intermediate conditions are marked together as *H* and *L*. A crude picture of the geographical trend can be drawn by listing and classifying the series studied from that segment of the range bounded by Alaska, Washington, Alberta, and western Montana. ALASKA: Sitka (LH); Ketchikan (lh, 2 series; Lh, 1 series); Metlakatla (Lh); Forrester Is. (Lh, 2 series, LH, 1 series); Wrangell (lh, 2 series); Port Beauclerc, Kuiu Is. (Lh); Point Barrie, Kupreanof Is. (lh). BRITISH COLUMBIA: Penticton (LH); Terrace (LH, 1 series; Lh, 1 series); Victoria Chase (LH); Keremeos (LH); Glacier (lh); Chilliwack Valley (lh); Howser, Selkirk Mts. (LH); Royal Oak, Vancouver Is. (LH); Alert Bay, Vancouver Is. (lH). ALBERTA: Red Deer (LH); Macleod (LH). WASHINGTON: Pullman (LH); Seattle (LH); Bay Center (Lh); Three Brothers Mt., Olympic Range (lH); Tacoma (LH); Metaline Falls, Pend Oreille Co. (LH); Milan, Spokane Co. (LH). IDAHO: Troy, Latah Co. (LH); south slope of Moscow Mt., Latah Co. (over 100 colonies examined in the field, nearly all LH, see below); Hyndman Creek, Challis Nat. For., Blaine Co. (lh). MONTANA (western half): St. Mary, Glacier Co. (lh); Flathead Lake (LH); Phillipsburg, Granite Co. (Lh); Troy, Lincoln Co. (LH); Sula, Ravalli Co. (LH).

Beyond this area, to the south and east, the two extreme characters *l* and *h* become much rarer, constituting less than 5 per cent of the total population. Following are the exceptional records in which they do occur. OREGON: Anthony Lake, Blue Mts., near Pendleton, 7000 feet (lh). CALIFORNIA: Lake Tahoe (Lh). WYOMING: Isa Lake, Yellowstone Nat. Pk., 8300 feet (Lh, 2 series). NEW MEXICO: Hyde State Park, Santa Fe Co., 8600 feet (Lh, 2 series); Ute Park, Colfax Co., 7400 feet (lH, 1 series; LH, 1 series); 15 miles north of Eagle Nest, Colfax Co., 9500 feet (lh).

It appears that *l* and *h* occur at least partly independent of one another, that they are most frequent in the extreme Northwest, and that they diminish southward and eastward. Beyond these limited data, there is some evidence to suggest that *l* at least may be environmental in origin. In six out of the seven records for *l* cited from south of Washington and Montana, the colonies were found at what probably represents the upper elevational limit for *sitkaensis* in each area. The Isa Lake series, for example, were taken by myself in spruce-fir woods at 8300 feet on the south slope of Craig Pass, well above the next highest record for the genus in Yellowstone Park (6800 feet). Both colonies were small, composed of nanitic workers, and situated under rocks in clearings in the forest; they were the only *Lasius* found in the vicinity and gave every impression of living under conditions of marginal existence. An incipient colony of similar type was taken at 5300 feet on Moscow Mountain, Idaho, well above the bulk of the dense *sitkaensis* population resident on this mountain. The workers of this colony were much darker than those taken from colonies at lower elevations, including another incipient colony found at 3500 feet. In the light of this evidence I consider that the extreme dark coloration (*l*) may be due partly or wholly to some environmental feature of high elevation such as lower temperature. There may be in effect a high elevation ecophenotype characterized by depauperate colonies of dark, nanitic workers and comprising a regular feature of populations in mountainous areas.

DISTRIBUTION. *L. sitkaensis* has the northernmost distribution of all the Nearctic members of the genus (Fig. 4). It occurs from eastern Quebec to southeastern Alaska, south in the East to Massachusetts, with an isolated population in the southern Appalachians of North Carolina, and south in the West to the San Jacinto Mountains of southern California and the higher isolated ranges of southern Arizona.

The extreme northeastern record is the mouth of the Matamek River, Quebec, on the north coast of the Gulf of St. Lawrence (H. Eidmann leg.; USNM). I have seen numerous series from throughout the maritime provinces of Canada, including New Brunswick, Nova Scotia (with Cape Breton Island), and Prince Edward Island. The species ranges over Maine, reaching the extreme southeast of the state at Saco and Kittery Point (MCZ); a random collection of *Lasius* made at the former locality for me by W. L. Nutting indicates that *sitkaensis* is far outnumbered there by *L. neoniger*. A single collection of winged reproductives in flight has been made at Marblehead, Mass. (G. C. Wheeler leg.

and Coll.), but the species must be rare this far south, because I have never collected it myself in the course of many field trips in eastern Massachusetts. It occurs in New Hampshire (Mt. Washington summit, male; C. S. Bacon leg., MCZ; Bowman and Bretton Woods, White Mts., E. O. Wilson and W. L. Brown leg., MCZ; lower east slope of Mt. Monadnock, W. L. Brown leg.,

Fig. 4. An outline of the known distribution of *L. sitkaensis*. (This and subsequent outline maps used with permission of the University of Chicago Press.)

MCZ) and Vermont (Proctor Piper State Forest; W. S. Creighton leg. and Coll.). I found a single colony in the midst of a dense *neoniger* population at Plattsburg, upper New York, and I have seen specimens from Lanesville, Catskill State Park, in the same state (K. Christiansen leg.; MCZ).

The southern Appalachian population represents a remarkable case of discontinuous distribution. Several colonies were found by A. C. Cole, A. Van Pelt, and myself in the summer of 1951 along the Blue Ridge Parkway northeast of Ashville, North Carolina, in the vicinity of Mt. Mitchell and nearby Craggy Gardens. These were all under rocks at the edge of spruce-fir and beech forests at elevations between 5000 and 5200 feet. This elevation range happens to include the upper limit for *L. neoniger* in the area, although this species still vastly outnumbers *sitkaensis* there. *Neoniger* shows a predilection for open situations and is the dominant ant along the grassy roadstrips. *L. alienus* occurs sporadically in rotting wood at the forest border. That the *sitkaensis* at this locality really belong to a restricted and completely isolated population is supported by considerable evidence. The northeast population obviously thins out in a southward direction in New England. I have never encountered it among the thousands of series of *Lasius* I have examined from the intervening area. It was not found in the exhaustive collection of ants made by Cole in the Smoky Mountains of Tennessee, and neither Cole, Van Pelt, nor have I ever taken it in the course of many field trips in the adjacent lowland areas of North Carolina and Tennessee. It remains to be seen whether other populations occur under isolated circumstances and at suitable elevations elsewhere along the course of the Appalachians.

West of New England, *sitkaensis* has been taken at several localities in Michigan and probably occurs over most of the state. I found a single colony in sand dune country near Marquette, on the northern peninsula, again inclosed in a dense population of *neoniger;* several other collections made by others in the same area suggest that it is a common species there. The southernmost record for the state is the Edward S. George Reserve, Livingston Co. (M. Talbot leg. and Coll.). Dr. Talbot's collections, made in conjunction with her recent intensive study of the ant fauna of the Reserve, have revealed *sitkaensis* to be an uncommon species there, greatly outnumbered by both *neoniger* and *alienus*.

Sitkaensis probably occurs over all of Minnesota; it was abundantly represented in a large collection of the genus made by Kenneth Kraft in Itasca State Park. I have seen a single series from Dickinson Co., Iowa, but the species must be rare this far south, since it was not present in a substantial collection made by R. L. King in several areas of Iowa, including Dickinson County. The species is apparently abundant over all of North Dakota, as indicated by the multitude of collections made over the past twenty-five years by G. C. Wheeler and his students. It has been taken on two occasions at Hill City, South Dakota (T. Ulke leg., MCZ; Creighton leg. and Coll.).

The records from Alaska to Washington and eastern Montana have been listed in the previous section on geographic variation. In the western United States *sitkaensis* is abundant along the entire length of the Rockies and Cascade-Sierras. It has been taken as far south as the Tanquitz Valley of the San Jacinto Mts., Calif. (USNM); Ramsey Canyon, Huachuca Mts., Ariz.; Rustler Park, Chiricahua Mts., Ariz.; and Hospital Flat, Graham Mt., Ariz. (the last three W. S. Creighton leg. and Coll.). It also occurs on isolated forested mountains through the Great Basin. Judging from many collections mostly by A. W. Grundmann (in Cole Coll.) it is abundant on the mountains and in the moist canyons around Salt Lake City, Utah. It has also been taken at Zion National Park, Utah (Creighton leg. and Coll.); Maggie Basin, Nev. (F. M. Gaige leg.; UMMZ); Lehman Caves, Mt. Wheeler, Nev. (Creighton leg. and Coll.); and Pole Canyon, East Humboldt Mts., Nev. (Creighton leg. and Coll.).

At Moscow Mountain (Idaho), Yellowstone Park, and the San Francisco Peaks (Ariz.), where I was able to study large populations first-hand, I found this species most abundant in the fir-yellow pine transition, sparser in the middle third of the fir belt, and rare in the upper third of the fir belt. Below the fir it extends into the pure pine forest and may be locally abundant there, even under relatively dry conditions.

ECOLOGY. My own studies of *sitkaensis* in the field, combined with abundant field notes supplied me by A. C. Cole, Kenneth Kraft, G. C. Wheeler, and others, show that this species is primarily a forest dweller, nesting in rotting logs and stumps and under stones. It penetrates forest clearings secondarily and is abundant, at least locally, in the almost treeless plains of central and western North Dakota (P. B. Kannowski, Joe Davis, R. P. Uhlmann; material in G. C. Wheeler Coll. and UMMZ) and southern Idaho (A. C. Cole). In the latter situation it usually nests under stones but occasionally constructs irregular soil craters removed from any ground cover. At Moscow Mountain, Idaho, I found hundreds of nests in rotting wood and under stones within the forest margin, but only one associated with a crater in open soil. In Itasca State Park, Minn., Kraft found six colonies associated with craters, out of sixteen collected. Cole, in collecting *Lasius* from a wide diversity of habitats in New Mexico, took *sitkaensis* most consistently under stones in moist, shaded soil. At Cloudcroft, New Mexico, and the San Francisco Peaks, Arizona, I found the species most abundant well back in the shaded portions of the forest, nesting almost exclusively under stones. In the White Mountains of New Hampshire, however, *sitkaensis* populations are densest nesting under stones in overgrown meadows on the lower slopes, and are less abundant under stones in the adjacent spruce-fir-larch forest.

Local populations of *sitkaensis* and its relatives *neoniger*, *alienus*, and *crypticus* are often spectacularly dense. It seems inevitable that some amount of interspecific competition must result, and it is therefore not surprising to find a tendency for these species to replace one another ecologically where they occur together. Near Bemidji, in central Minnesota, I found *sitkaensis* in a deciduous woodlot nesting in rotting logs and stumps, a niche usually occupied by *alienus* in localities farther east where *sitkaensis* is rare or absent. *Neoniger* prevailed in adjacent open areas. At Kiowa, Montana, *sitkaensis* again seemed to replace *alienus* in deciduous woods; *crypticus* was abundant in an adjacent subalpine meadow, while *neoniger*, its nearest ecological equivalent, was absent. At Moscow Mountain and Cloudcroft, *sitkaensis* occurred in exceedingly large numbers, apparently to the exclusion of other members of the subgenus.

The food habits of *sitkaensis* are evidently generalized. Kannowski (*in litt.*) has found workers on several occasions associated with aphids in galleries under rocks, while at Moscow Mountain I observed workers carrying dead and crippled insects back to their nests during the early part of the night. A colony maintained under observation at the Harvard Biological Laboratories for nearly two years has readily accepted both honey and dead and crippled insects.

Winged forms have been taken in the nests from July 4 (Neche, Pembina Co., N. Dak.; E. L. Krause leg.; G. C. Wheeler Coll.) and July 7 (Cloudcroft, N. Mex.; W. M. Wheeler leg.; MCZ) to September 24 (Lodema, Pembina Co., N. Dak.; Krause leg.; G. C. Wheeler Coll.). The great majority of *in nido* records are from August. G. C. Wheeler took pairs flying in copula at Marblehead, Mass., on September 3, 1927, and N. A. Weber took a pair in copula at Towner, McHenry Co., N. Dak., on August 18, 1927 (both G. C. Wheeler Coll.). Eidmann (1933) observed nuptial flights of "*americanus*" (probably the *sitkaensis* already referred to) in the Matamek region of Quebec on September 4. Borys Malkin found stray dealate queens at Wrangell, Alaska, in the first week of August.

LASIUS BRUNNEUS (Latreille)

(Subg. *Lasius*)

Formica brunnea Latreille, 1798, Essai Fourmis France, p. 41; worker; original description. Type locality: France.

Formica pallida Latreille, 1798, *ibid.*, p. 41; worker; original description. Type locality: France. NEW SYNONYMY.

Formica brunnea var. *pallida*, Latreille, 1802, Histoire Naturelle des Fourmis, p. 169.

Lasius niger var. *alieno-brunneus* Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 47; worker; original description. Synonymized by Stärcke, 1944, Ent. Ber., **11**: 156–157.

Lasius niger brunneus var. *himalayana* Forel, 1894, Jour. Bombay Nat. Hist. Soc., **8**: 404; worker; original description. Type locality: Himalayan Mts., 6000–9000 feet. NEW SYNONYMY.

Lasius niger var. *himalayanus*, Forel, 1917, Bull. Soc. Vaud. Sci. Nat., **51**: 725.

Acanthomyops brunneus var. *nigro-brunneus* Donisthorpe, 1926, Ent. Rec., **38**: 18; worker. Type locality: Italy. NEW SYNONYMY.

DIAGNOSIS. A distinct species characterized by large males with intermediate *sitkaensis-niger* type mandibles and workers with short scapes and sparse pilosity.

Worker. (1) Scape shorter relative to head width than in any other member of the subgenus (Fig. 5); SI 82-91 in all European series measured; 94 in the *himalayanus* lectotype and in one specimen from Lahore, Pakistan, both small specimens (see under geographic variation).

(2) Small individuals (PW 0.50-0.57 mm.), when viewed in perfect full face, with the lateral margins of the eyes not reaching the lateral borders of the head; in *niger* and *alienus* they reach or exceed it.

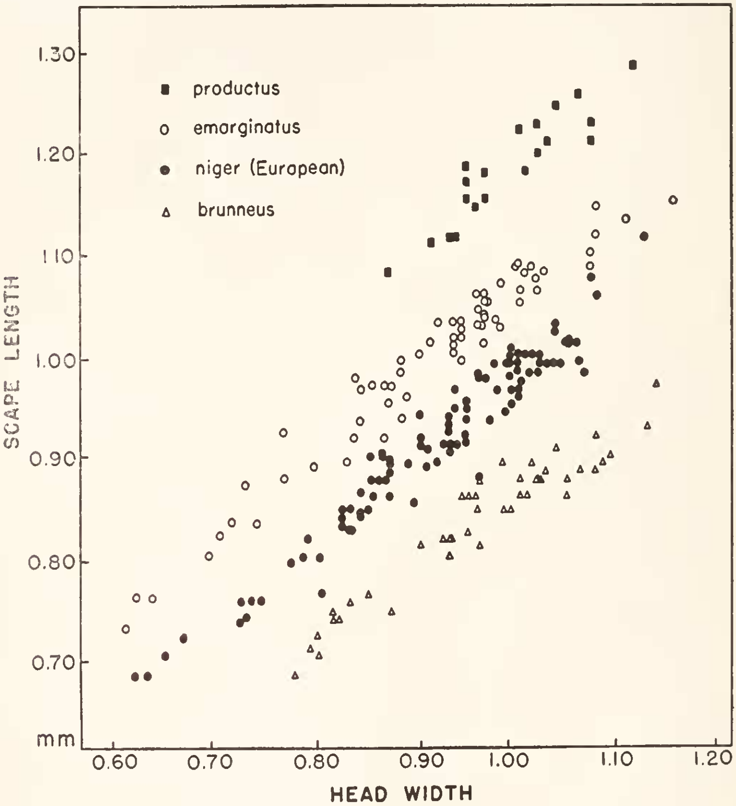

Fig. 5. Head width-scape length relationships in the worker caste of *L. brunneus* and the members of the *L. niger* complex. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

(3) Mandibles proportionately shorter, more incurved, and inserted slightly closer to the midline, and head more massive relative to the alitrunk, than other *Lasius s. s.* (Pl. 1, Fig. 9). Occipital margin viewed in full face flat to feebly convex, as opposed to the typically concave outline of *niger* and *alienus.*

(4) Mandible with only two basal teeth in all of seven nest series examined for this character.

(5) Scapes and tibiae completely devoid of standing hairs and nearly devoid of hairs of any inclination. Body pilosity sparse; the curving portion of the occipital angles viewed in full face typically devoid of hairs, rarely with one or two; the latter condition occurs in other members of the subgenus but is highly exceptional.

(6) Alitrunk and petiole homogeneous light reddish brown, rarely medium reddish brown, contrasting against the dark brown gaster. The head usually the same color, occasionally darkening to medium or dark reddish brown to contrast against the alitrunk. (*Niger* and *alienus* typically concolorous.)

Queen. (1) SI low; 68-71 in 9 individuals from 6 localities having HW 1.49-1.64 mm., and 76 in a smaller individual with HW 1.39 mm.

(2) Pilosity and mandibular dentition as in worker.

(3) Frontal suture well marked, set in the middle of a conspicuous broad, shallow trough.

(4) Color distinctive; body uniformly dark reddish brown, appendages a contrasting yellowish brown.

(5) Fore wings infumated in the inner and upper thirds.

Male. (1) Larger than other members of the subgenus, HW 1.04-1.10 mm.

(2) Mandibles of a type intermediate between *sitkaensis* and *niger:* there is a well marked subapical cleft as in *sitkaensis,* but it is set more posteriorly than in this primitive species; the basal angle is broadly rounded and the masticatory border lacks denticles, both of which characters are associated with the more advanced *niger* type.

(3) Frontal suture conspicuous as in queen.

(4) The entire dorsal petiolar margin involved in a deep concavity. In a series from Windsor Forest, Berks, England, secondary lateral convexities are present within this concavity.

(5) Parameres shorter relative to HW than in other members of the subgenus (Fig. 7).

FURTHER DESCRIPTION. *Worker.* Size range and dispersion probably about the same as in *niger.* In a sample of 29. with no more than 2 individuals per nest series, PW range 0.50-0.73 mm., mean with standard error 0.630 ± 0.012 mm., standard deviation 0.063 mm. ML less than EW. Anterior margin of median clypeal lobe and structure of the mandibular basal angle essentially as in the *niger* complex. The greater massiveness of the alitrunk in this species can perhaps best be expressed as a ratio of alitrunk length to the maximum head depth measured perpendicular to the long axis of the head. Several medium-sized *brunneus* gave such a ratio of 67-69, whereas *alienus* of comparable size ranged between 70 and 76. Viewed from the side the propodeal angle tends to be more acute and the declivitous face of the propodeum tends to be longer relative to the dorsal face than in other *Lasius s. s.* The dorsal margin of the petiole was invariably concave in all series examined; occasionally the concavity is so deep as to be nearly semicircular.

Male. SI of several individuals measured 60-64, overlapping part of range of variation of *niger* (*q. v.*). ML 0.15-0.17 mm., overlapping part of ranges of *niger* and *emarginatus.*

GEOGRAPHIC VARIATION. Series examined were too limited in number and distribution to give a clear picture of geographic variation. One trend is suggested by the fact that two of the three Asiatic specimens examined had a SI above the range of variation of the European sample; these were a single specimen from Lahore, Pakistan, and one of two *himalayanus* syntypes.

DISTRIBUTION. *Brunneus* is widely distributed in western Europe, reaching south to North Africa and eastward to the western Himalayas. Below are listed the records which have been verified in the course of the present revision.

ENGLAND: Windsor Forest, Berks (H. Donisthorpe leg.; specimens in MCZ, USNM, and several private European collections); Chadbury, Worcestershire (C. S. Collingwood leg. and Coll.). NORWAY: Ullern, near Oslo (H. Holgersen leg. and Coll.). SWEDEN: Stockholm (K.-H. Forsslund leg. and Coll.). SWITZERLAND: Flawil (H. Kutter leg. and Coll.); Aarau

(Kutter Coll.); Freiburg (A. Forel leg.; MCZ). AUSTRIA: Vienna Forest (Wiener Wald) (MCZ). ITALY: Lipizza, near Trieste (B. Finzi leg.; MCZ). YUGOSLAVIA: "Podcetrtek" (not located) (Jaeger leg.; Holgersen Coll.); Bosnia (Reitter leg.; Holgersen Coll.). ALBANIA: Mali Daiti (Ravasini and Lona leg.; MCZ). U.S.S.R.: Krimea (W. Karawajew; MCZ). ALGERIA: no further data (Reitter leg.; Holgersen Coll.). PAKISTAN: Lahore (R. K. Enders leg.; Weber Coll.).

This species has been confused so often with *L. alienus* that literature records are of dubious value. Two have been encountered which are nevertheless of sufficient interest to deserve mention here: Puenta de la Reina, Navarra, Spain (Santschi, 1919); and Enzeli (Pehlevi), Iran (Crawley, 1920). These represent slight range extension if valid.

ECOLOGY. Most European authors agree that *brunneus* is a timid species adapted to living under the bark and in the wood of tree trunks. Donisthorpe (1927) found a large population of this species in the Windsor Forest of England limited to living trees, which the ants penetrated from the trunk up into the main branches and down into the roots. Various trees were inhabited, including oaks, elm, ash, beech, poplar and maple. It is not clear whether the workers carried on much excavation in the living wood, but this seems unlikely due to the rather unspectacular mandibular apparatus of the species. Forsslund (1949) found *brunneus* in oaks in dense, undisturbed woodland in several localities in the vicinity of Stockholm. The nests were mostly in dead wood, but occasional galleries penetrated living wood. Scherdlin (1909) found the species in Alsace nesting in the trunks of trees and timber of houses. Clausen (1938) observed a swarm of reproductives inside a house in Zurich. Gösswald (1932) states that in Germany *brunneus* is found as often under stones as in dead wood; since this observation is divergent from those of other authors, the possibility must be considered that he was erroneously including some *alienus* in his concept of *brunneus*.

Donisthorpe (*ibid.*), who has undertaken the most careful study of this species to date, found workers transporting and tending aphids of the genus *Stomaphis*. He also observed them carrying psocids and other small insects to the nests, presumably for use as animal food.

Brunneus appears to hold its nuptial flights earlier in the day and season than other European members of the subgenus. Donisthorpe (*ibid.*) encountered winged queens and males swarming over the trunk of an oak at noon on June 25, and Forsslund (*ibid.*) saw the same thing from noon to 1:30 p.m. during the period June 10-16.

SYNONYMY. *Formica pallida* Latreille and *Acanthomyops brunneus* var. *nigro-brunneus* Donisthorpe appear to represent the two extremes of normal color variation in *brunneus* and to be without any geographic significance.

Lasius brunneus var. *himalayanus* Forel. Lectotype by present selection, a worker in the AMNH. PW 0.56 mm., HW 0.78 mm., SL 0.73 mm., SI 94. A syntype presumably from the lectotype nest series has been placed in the MCZ and gives the following measurements: PW 0.64 mm., HW 0.97 mm., SL 0.86 mm., SI 89, ML 0.17 mm., EW 0.19 mm. The differences in size, color and pubescence given by Forel are actually insignificant. The lectotype and syntype seem to be well within the normal range of variability of European *brunneus* in every character with the one exception of the high SI of the lectotype.

[Lasius schiefferdeckeri Mayr]

(Subg. *Lasius*)

Lasius schiefferdeckeri Mayr, 1868, Beitr. Naturk. Preuss., Phys.-ökon. Ges. Königsberg, **1**: 44–46; pl. 1, fig. 2; pl. 2, figs. 27–32; worker, queen, male; original description.

Lasius edentatus Mayr, 1868, *ibid.*, pp. 46–47; male; original description. NEW SYNONYMY.

Lasius schiefferdeckeri, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, **55**: 120.

DIAGNOSIS. This is the predominant *Lasius* of the Baltic amber deposits. Wheeler (1914) offered the opinion that *schiefferdeckeri* is very close to the modern species *L. alienus* (''*niger* var. *alienus*'' and ''*americanus*''), differing only by its smaller size. The present study has shown that size differences are actually insignificant but that *schiefferdeckeri* does exhibit variation in scape index transspecific for most of the modern members of the *niger* complex, as well as a peculiar male mandible structure intermediate between the primitive *sitkaensis* type and advanced *niger* type.

Worker. (1) Size range and mean, clypeus, mandibular dentition, and appendage pilosity similar to *alienus.*

(2) ML exceeding EW.

(3) SI very variable, ranging in value from typical *emarginatus* through typical (northern European) *niger* to typical *brunneus.*

Queen. No specimens were seen during the present study. A figure of the head by Mayr is somewhat diagrammatic but shows a *niger*-type clypeus and mandibular dentition as opposed to the distinctive *sitkaensis* types.

Male. (1) Very small, at lower limit of *alienus* size variation.

(2) Mandible form showing great variation which brackets both the *sitkaensis* and *niger* types, a condition also encountered in the modern species *L.* (*Cautolasius*) *flavus* (see under further description of *schiefferdeckeri* below).

SYNTYPES. The only specimens designated as types by Mayr were several males inclosed in a single piece of amber in the Menge Collection (Leipzig). These were given as the source of his male diagnosis ("Typen bei der Diagnose") and described as having denticulate mandibles. From this information and by inference from comparison with the description of *L. edentatus,* we may assume that these males had *sitkaensis*-type mandibles, with a well defined basal angle and denticulate masticatory border, which characters can now be shown to fall at one extreme of the *schiefferdeckeri* variation.

MATERIAL STUDIED. Eleven workers and three males in the William A. Haren Collection (MCZ).

FURTHER DESCRIPTION. In the present study each piece of amber was planed and polished at several angles to allow precise measurement of the essential structures. As a result, descriptions of these fossil specimens are probably nearly as accurate as those of modern material, and their status relative to modern species can be discussed with some confidence.

Worker. Individual measurements of each of the eleven workers are given in the accompanying table. It will be noted that even in this small sample the scape index is extraordinarily

Variation in Critical Characters in *Lasius schiefferdeckeri* Mayr (Workers)

Specimen	PW (mm.) (or estimate of size)	$\frac{SL}{HW}$	SI	SI regression line fit	ML (mm.)	dentition	anterior clypeal border	seta count
1	very small, lower *alienus* limit			approaching *brunneus*		*niger*-type (probably only 2 basal teeth)		0?
2	0.50							1
3	0.46	$\frac{0.71}{0.68}$	105	*niger* lower limit	0.18 (EW=0.14)			0
4	0.69	$\frac{0.96}{0.93}$	103	*niger* upper limit	0.21 (>EW)			0
5	0.50	$\frac{0.83}{0.77}$	108	*niger-emarginatus* int.		*niger* type		0?
6	0.43	$\frac{0.60}{0.69}$	87	*brunneus*				0?
7	0.64	$\frac{0.92}{0.86}$	107	*niger-emarginatus* int.	0.22 (EW=0.21)	*niger* type (only 2 basal teeth)	*niger* type	0
8	0.61	$\frac{0.87}{0.93}$	94	*niger-brunneus* int.				0
9	small	$\frac{0.80}{0.66}$	121	*emarginatus*				0
10	0.54	$\frac{0.84}{0.84}$	100	*niger*	EW(?)			0
11	0.48	$\frac{0.87}{0.83}$	104	*niger-emarginatus* int.	EW(?)			

variable in comparison to modern species. That we are dealing with a single species in the amber material is evidenced by the lack of any tendency to grouping in the SI values, plus the uniformity of the palpal and pilosity characters. For instance, in no. 3, a low SI is combined with a high ML, and in nos. 5, 7, and 9, a high SI is combined with *alienus*-like pilosity; both situations are consistent with the reminder of the sample but unlike anything found in modern populations.

Characters additional to those in the chart may be mentioned. The CI is 100 in no. 6, 93 in no. 7, 89 in no. 9, 95 in no. 10, and 88 in no. 11. This also represents an unusual amount of variation for a single species, even when the considerable amount of overlap betwen the regression zones of modern species is taken into account. The SI and CI are concordant in every case but no. 9, which has an *emarginatus* SI and *niger* CI. The dorsal margin of the petiole seen in frontal view shows the same type of variation as in modern members of the subgenus, ranging from weakly concave to weakly convex.

Male. Specimen no. 1. Subapical cleft of mandible present but shallower than in *sitkaensis;* masticatory border flat; basal angle intermediate in development between *sitkaensis* and *niger*. HW 0.77 mm., SI 85. SI very high with respect to modern members of the subgenus, above the *emarginatus* range but still below that of *productus*. Paramere similar in proportionate size and shape to that of *alienus*.

Specimen no. 2. Mandible partly decomposed and further obscured by a fissure, apparently with a well-developed spical cleft and basal angle. Size somewhat smaller than no. 1. Paramere similar in proportionate size and shape to that of *alienus*.

Specimen no. 3. Subapical cleft present but set about one-third back from the apex, an intermediate *sitkaensis-niger* condition occasionally seen in *L. flavus* and rarely in *L. alienus*. Basal angle weakly developed, close to *niger* type. HW *ca*. 0.66 mm.

The diagnostic character given for *L. edentatus* Mayr, based on a single amber male, was the absence of denticulae and distinct basal angle on the mandible. I have synonymized this species on the assumption that the great variability in the male mandible in the three specimens just described and the intermediate *sitkaensis-niger* condition of two of them indicates total variability similar to that seen in *flavus,* i.e. ranging from the *sitkaensis* type all the way to a condition closely approaching the *niger* type. In fact, the three specimens by themselves encompass about three-fourths of the total possible variation. I cannot attach any significance to the fact that Wheeler himself failed to find such a transition in the 20 males he examined. When he states ''I have found no specimens agreeing with this description [*edentatus*], either in the Geolog. Inst. Koenigsberg Coll. or in the Klebs Coll.'', he is giving the unintentional but erroneous impression that all 20 specimens were examined for the diagnostic character. Actually, he was probably unable to see the mandible outline in the majority of specimens he examined. Nearly every specimen in the already-prepared Haren material which I studied had to be reground and repolished before a favorable view was obtained; there is no evidence that Wheeler ever made preparations of this sort during his own study.

FAUNAL RELATIONSHIPS. *L. schiefferdeckeri* was apparently one of the most abundant ants of Baltic amber times, since it composed 1172 out of the 11,678 amber specimens collectively studied by Mayr, André, and Wheeler (Wheeler, 1914). It was surpassed in this respect only by *Iridomyrmex goepperti* (Mayr), *I. geinitzi* (Mayr), and *Formica flori* Mayr. Wheeler found workers included in the same block of amber with *Iridomyrmex goepperti* and *Formica constricta.* In the absence of further data it may be contended that *Lasius schiefferdeckeri* was a member of a warm temperate fauna, possibly segregated by elevation or latitude in the extensive amber forest region. Its presumed derivative species, the members of the modern *niger* complex, have continued to thrive in the Palaearctic Region, along with species of *Stenamma, Leptothorax, Formica,* and *Prenolepis,* at the same time that numerous other amber genera have withdrawn to tropical regions or declined to total extinction.

[Lasius pumilis Mayr]
(Subg. *Lasius*)

Lasius pumilis Mayr, 1868, Beitr. Naturk. Preuss., Phys.-ökon. Ges. Königsberg, 1: 46; pl. 2, fig. 33; worker; original description.

Lasius punctulatus Mayr, 1868, ibid., p. 46; pl. 2, fig. 34; queen; original description. NEW SYNONYMY.

Lasius pumilis, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, **55:** 122–123.

Lasius pusillus [!], Wheeler, 1914, *ibid.,* p. 142.

DIAGNOSIS. A tiny Baltic amber species with no close living relatives. The worker caste resembles superficially that of the modern species *L. sitiens* Wilson but can be distinguished from it readily on the basis of palpal and dentition characters.

Worker. (1) Exceedingly small, PW under 0.30 mm. in the two specimens examined.

(2) Alitrunk completely lacking standing hairs.

(3) Funicular segments II, III, and IV slightly broader than long. Length of maxillary palp segment VI (ML) exceeding the EW.

(4) Mandibles with only one basal tooth in the single specimen which could be examined for this character.

Queen. Assuming that *punctulatus* is the queen of *pumilis,* as all the evidence seems to indicate, this caste is distinguished from that of all other *Lasius s. s.* by its extremely small size. Total length, according to Mayr, 3.0-3.8 mm.

SYNTYPES. Three specimens were mentioned by Mayr in the original description, one each in the Königsberg Geological Institute Collection, Menge Collection, and Mayr Collection.

MATERIAL EXAMINED. Two workers in the William A. Haren Collections (MCZ).

FURTHER DESCRIPTION. *Worker.* Specimen no. 1. PW 0.30 mm., HW 0.46 mm., SL 0.48 mm., SI 105, CI 92, ML 0.11+ mm., EW 0.10 mm. Funicular segments II, III, IV broader than long. ML exceeding the maximum width of the fore tibia, thus markedly longer than in the small modern species *sitiens.* Eye with only 12 ommatidia but not noticeably reduced proportionate to total head size. Mandibles relatively small, giving the head an unusually rounded appearance when viewed in full face. Anterior margin of the median clypeal lobe with straight lateral faces but with a broadly rounded middle so that an outline intermediate between the *niger* and *neoniger* conditions is obtained. Petiole broadly spatulate in frontal view, with gradually rounded dorsal corners and flattened dorsomedian margin.

Specimen no. 2. HW 0.41 mm., SL 0.45 mm., SI 109, CI 93, ML 0.14 mm. (greater than estimated EW). Funicular segments II, III, and IV broader than long. Mandibular dentition of elementary formicine type (see under Terminology and Measurements) but with only one basal tooth.

A conflict exists between Mayr's description and figure of this species: funicular segments II, III, and IV are stated to be broader than long, but the figure shows II and III longer than broad. The description is probably more accurate, as indicated by the two specimens measured in the present study.

[LASIUS PERITULUS (Cockerell)]
(Subg. *Lasius*)

Tetramorium peritulum Cockerell, 1927, Ann. Mag. Nat. Hist., (9) **19**: 165; male; original description.

Lasius peritulus, Carpenter, 1930, Bull. Mus. Comp. Zool., **70**: 58.

DIAGNOSIS. This is the *Lasius s. s.* species of the Florissant shales, which deposits are considered lower to middle Oligocene in age (MacGinitie, 1953) and the best North American counterpart of the Baltic amber so far as the preservation of insects is concerned. I have had the opportunity to study the excellent collection of *peritulus* arranged by Prof. F. M. Carpenter at the Museum of Comparative Zoology at Harvard University. Despite the fact that these specimens represent finely preserved rock fossils, they are still far inferior to the amber material and cannot be determined accurately beyond placement within the *niger-neoniger* species group.

Queen. Of 129 specimens examined, 5 were in a position to show the basal angle of the mandible, which is the crucial diagnostic structure in the subgenus. Each of the 5 possessed a "*niger*-type" mandible (see under description of *niger*), with the basal tooth as large as the adjacent teeth and aligned with them. Although the material is too badly crushed to allow precise measurements, the total size appears small, toward the lower limit of the range of size variation in *niger*.

Male. Of 91 specimens examined, 5 showed the entire mandibular outline. In each case this was unmistakably the "*niger* type", with the masticatory border shallowly impressed in its distal half, the basal angle broadly rounded, and the preapical cleft lacking. Two other specimens showed only the basal angle, which was also broadly rounded. The total size is approximately the same as for the modern Nearctic populations of *niger* and *alienus.*

HOLOTYPE. According to Carpenter, the unique type is a well preserved male now located in the British Museum.

LASIUS NIGER (Linnaeus)
(Subg. *Lasius*)

Formica nigra Linnaeus, 1758, Syst. Nat., Ed. 10, **1**: 580; worker; original description. Type locality: Europe.

Lasius niger, Fabricius, 1805, Systema Piezatorum, p. 415.

Lasius niger var. *alieno-niger* Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), pp. 47, 49; worker, queen; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger aliena var. *alieno-nigra*, Emery, 1925, Genera Insect., fasc. 183, p. 230.

Lasius alienus alieno-niger, Zimmermann, 1930, Verh. Zool.-bot. Ges. Wien, **84**: 48.

Lasius niger var. *alienoides* Emery, 1891, Explor. Sci. Tunisie, Paris (Impr. Nat.), p. 16; worker; original description. NEW SYNONYMY.

Lasius niger flavescens Forel, 1903, Ann. Mus. Zool. Acad. Imp. Sci. St. Petersburg, **8**: 386–387; worker; original description. Type locality: Bukhara, Uzbek S. S. R., Soviet Central Asia; by present selection. NEW SYNONYMY.

Lasius niger emeryi Ruzsky, 1905, Formicariae Imperii Rossici (Schrift. Naturforsch.-Ges. Univ. Kasan, vol. 38), pp. 313–314; worker; original description; In Russian. Type locality: Pamirs, Tadzhik S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger nitidus Kuznetzov-Ugamskij, 1927, Rev. Russ. Ent., **21**: 188; worker; original description. Type locality: Kara-su River, 65 km. northeast of Tashkent, Uzbek S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger alienus var. *pilicornis* Kuznetzov-Ugamskij, 1927, *ibid.*, p. 189; worker; original description. Type locality: Zailiski Ala Tau Mountains, near the city of Alma Ata, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger var. *minimus* Kuznetzov-Ugamskij, 1928, ''Ants of the South Ussuri Region'' (in Russian), U.S.S.R. National Geographic Society Publications, p. 20; worker; original description. Type locality: Okeanskaja Railroad Station, near Vladivostok, Soviet Maritime Territory. NEW SYNONYMY.

Lasius emarginatus var. *nigrescens* Stitz, 1930, Mitt. Zool. Mus. Berlin, **16:** 240; queen; original description. Type locality: Maz, Westl. Täler, Pamirs, Tadzhik S. S. R., 3580 meters. NEW SYNONYMY.

Lasius niger coloratus Santschi, 1937, Bull. Ann. Soc. Ent. Belg., **68:** 387; worker, queen; original description. Type locality: Musha, Formosa; virtual selection by Santschi, 1941, ref. below. NEW SYNONYMY.

Lasius emarginatus var. *japonicus* Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18:** 277–278; worker; queen; original description. Type locality: Tokiawa, Hokkaido; by present selection. NEW SYNONYMY.

Lasius transylvanica Röszler, 1943, Zool. Anz., **144:** 44–46; worker, male; original description. Type locality: Nyárádtö, Rumania. NEW SYNONYMY.

Lasius transsylvanicus [!], Stärcke, 1944, Ent. Ber., **11:** 157.

Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 420, *part*. [*nec neoniger* Emery 1893].

DIAGNOSIS. The worker is best distinguished by its abundant standing appendage pilosity combined with the clypeal outline and mandibular dentition characteristic of the "*niger* complex" (*niger, alienus, emarginatus, productus*). Over most of Europe and in western North America *niger* has a scape index regression zone intermediate between those of *brunneus* and *emarginatus,* but in peripheral Eurasian populations this zone shifts to overlap that of *emarginatus*. The male is best distinguished by the possession of abundant standing pilosity on the appendages combined with the "*niger* type" mandible described below.

Worker. (1) More than 95 per cent of the workers within HW range 0.61-1.21 mm., exclusive of material from North Africa, the Balearics, Azores, Madeira, and eastern Asia, possess a SI between 95 and 103. This is a strongly allometric character (Fig. 5), with minimas (HW less than 0.61 mm.) ranging up to 109.

(2) As a corollary to (1), ML within this sample exceeds EW.

(3) Mandibular dentition characteristics of the *niger* complex: basal teeth two to four in number, equal in size, and spaced at even intervals; opposed to the *neoniger* complex, in which the two or three basal teeth are irregularly spaced and the central one of a set of three is often reduced in size.

(4) Clypeus characteristic of the *niger* complex: when the mandibles are opened and the head is viewed in perfect full face, the anterior border of the median clypeal lobe describes an even,

broad parabolic curve, with the sides at least feebly convex and only occasionally meeting in a point at the midline; opposed to the more angular clypeal border of the *neoniger* complex. (See Pl. 1, Figs. 2 and 3.) The clypeus is usually, but not always, keeled.

(5) Scapes and tibiae always with abundant standing pilosity, except in minimas with PW less than 0.47 mm. The inclination and density of this pilosity show striking geographic variation (see below). In general, *niger* complex workers with seta counts greater than 25 are almost certainly *niger,* but those with less might be *alienus* and should be determined with the aid of the allometry regression zones plotted in Figure 6.

Queen. (1) Within the geographic limits stated in the first worker character above, queens with HW between 1.54 and 1.82 mm. have an SI between 72 and 80.

(2) As a corollary to (1), queens within this sample have a ML between 0.17 and 0.23 mm., with over 90 per cent falling within 0.18-0.21 mm.

(3) Clypeus and mandibular dentition as in worker.

(4) Scapes and fore tibiae with abundant standing hairs; seta count usually over 20 and often over 40. Inclination and density subject to geographic variation as in worker.

(5) Wings hyaline except for a small area distal to the axillary sclerites; this is a general *niger* complex character.

Male. (1) Within the geographic limits stated in the first worker character above, SI 62-69, ML 0.14-0.16 mm.

(2) Mandible characteristic of the *niger* complex: primitive preapical cleft of *sitkaensis* and *brunneus* modified into a shallow angular depression placed centrally on the masticatory border or lacking altogether, so that the masticatory border curves gently inward from the apex and then outward to meet the basal border. The basal angle broadly rounded, the masticatory border curving gradually into the basal border. Denticles lacking on the masticatory border. (See Pl. 1, Fig. 5.)

(3) The subgenital plate subrectangular, the posterior sclerotized, setiferous lobes not more than one-fourth as wide across their base as the plate itself but protruding past the unsclerotized posterior rim and reaching as far back as the level of the tips of the posterolateral flanges. A single series from Shriek, Belgium (A. Raignier leg.; MCZ), contains individuals with two

distinct lobes, a single lobe, and several stages intermediate in the coalescence of two lobes.

(4) Long standing hairs present over most of the surfaces of the scape and fore tibia, but much sparser than in the worker and queen; seta count usually less than 5.

(5) Size (see under geographic variation).

FURTHER DESCRIPTION. *Worker.* In a sample of 165, with no more than 2 per nest series, PW range, 0.40-0.83 mm., mean with standard error 0.630 ± 0.005 mm., standard deviation 0.069 mm.

Thirty-four individuals each representing a different nest series were examined especially for dentition; 27 had three basal teeth, 5 had four, and 2 had four with the antepenultimate tooth reduced in size; one lacked the second intercalary tooth.

Petiole outline more variable than in other members of the subgenus. Among 52 nest series examined especially for this character, the dorsal border was gently convex in 14, straight in 11, roundly concave in 22, and angularly concave in 5.

In a strong, reflected, artificial light, the body surface is subopaque to moderately shining. The degree of shininess varies inversely with the density of the pubescence and coarseness of the shagreened sculpturing, both independent and highly variable characters by themselves.

Body nearly or completely concolorous medium to blackish brown. Legs typically medium brown, scapes tending to yellowish brown.

GEOGRAPHIC VARIATION. Some amount of geographic variation has been found in appendage pilosity, appendage length, male size, and male genitalia, each of which appears to be genetically controlled and independent of the others.

Appendage pilosity. Throughout Europe, North Africa, and the adjacent Atlantic Islands, quantity of standing appendage pilosity varies in an allometric regression zone relative to head width as shown in Figure 6. This zone is sufficiently discrete from that of the sibling species *alienus* to allow a certain placement of nearly all of the enormous numbers of nest series examined during the present revision. In eastern Asia two changes occur in this character. If series from northern and western China, Manchuria, Korea, and Japan are plotted as a unit, the regression zone is seen to have shifted so that its lower end is

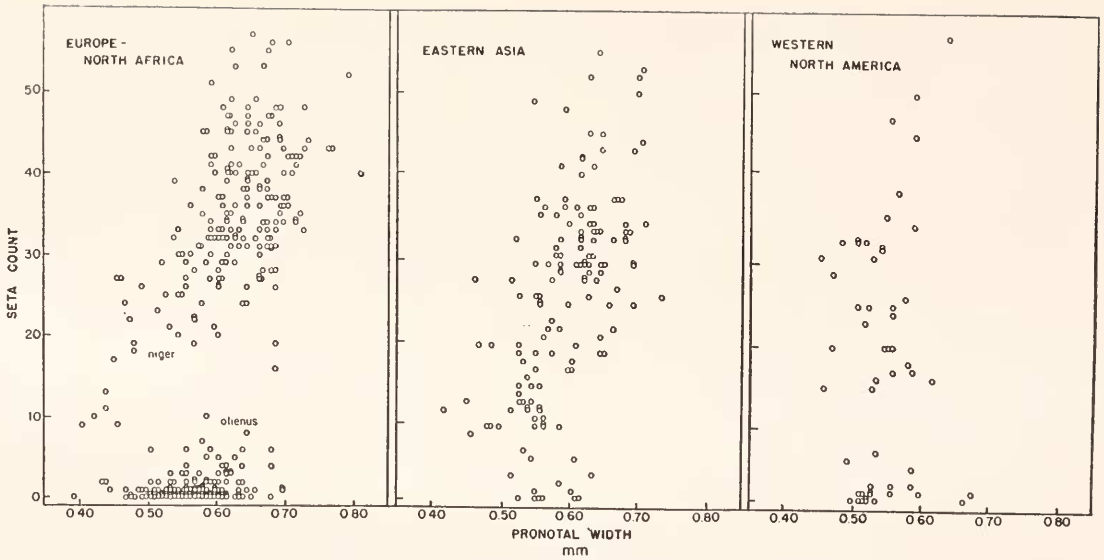

Fig. 6. Pronotal width-seta count relationships in the worker caste in three geographic samples of *L. niger* and *L. alienus*. This is the principal character used to separate these two closely related species. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

contiguous with and possibly overlapping the *alienus* zone (see also Fig. 6). As a result east Asian nest series comprised of smaller individuals (PW 0.47-0.59 mm.) often cannot be determined with assurance as either *niger* or *alienus*. In view of several other striking cases, in *Lasius,* of species convergence as a result of geographic variation, I do not think that this particular case is best interpreted as having arisen through interspecific hybridization, although this explanation is certainly available. Rather, I consider it significant that *alienus* is much rarer in Asia than in Europe, and it is my personal view that *niger* converges morphologically toward *alienus* in Asia because it is allowed to penetrate more of the usual *alienus* ecological niches there. No direct evidence is available to support such a view, but there does exist a fairly well documented precedent, to be described later, in the relationship between *Lasius flavus* and *L. nearcticus.*

Unfortunately, geographic variation in the seta count cannot be plotted precisely, locality by locality, on the basis of available material, because it is necessary for a given nest series to fall in the higher size range to show which regression zone it fits. Moreover, at least several individuals are needed to judge the character of the colony as a whole. About the most that can be said is that the seta count convergence appears to predominate in northeastern Asia, while lack of material makes it impossible to determine its westward extension. I have noted it in a single specimen from Naran, N. W. F. P., Pakistan (R. K. Enders leg.; Weber Coll.). One series each from Hu Hsien and Miao T'ai Tze, Shensi Prov., China (W. L. Brown leg.; MCZ) conform to the European population. Alate queens from Beh Luh Din, Szechwan Prov., China (D. C. Graham leg.; USNM) have relatively sparse appendage pilosity and may therefore conform to the northeastern Asian population.

In the mountains of western North America, *niger* exhibits a regression zone very similar to that of the northeastern Asian population, as shown in Figure 6. The regression in fact may be even steeper, approaching an almost perpendicular slope.

Another, more conspicuous pilosity change occurs in southeastern Asia: the scape becomes densely clothed with decumbent to subdecumbent hairs ¼ to ¾ as long as the greatest width of the scape, forty or more being counted along the single plane used in the seta count, and often dense enough to give a furry appearance. This character seems to predominate in Formosa and is occasional in Pakistan, Korea, Japan, and China. FORMOSA: Funkiko (3 series, F. Silvestri, J. Sonan, and L. Gressitt leg.; MCZ); Musha (*L. niger coloratus* Santschi cotypes); Rakuraku (S. Miyamoto leg.; Yasumatsu Coll.); Sakahen (Gressitt leg.; MCZ); Suisharyo (Gressitt leg.; MCZ). CHINA: "Yi Leang" (not located; Silvestri leg.; MCZ). KOREA: Suijen (Silvestri leg.; MCZ). PAKISTAN: Nathagali, N. W. F. P., 8200 feet (R. K. Enders leg.; Weber Coll.). JAPAN: Nagasaki (Michino-o), Kyushu (Silvestri leg.; MCZ); Hirooka, Shikoku (H. Okamoto leg.; Okamoto Coll. and MCZ). An intermediate condition, in which the oblique hairs decrease in number and the sub-erect and erect hairs increase, is seen in series from the following localities: Soochow, Kiangsu, China (N. G. Gee leg.; MCZ); Seoul, Korea (Yasumatsu Coll. and MCZ); Ikegawa, Shikoku (Okamoto leg. and Coll., MCZ); Okayama, Honshu (Silvestri leg.; MCZ); Hikosan, Kyushu (Yasumatsu leg. and Coll., MCZ).

Appendage length. Variation in this character shows a mosaic geographic distribution. As mentioned previously, most European material falls in the HW-SL regression zone illustrated in Figure 5. Material from the Balearics, Gibraltar, North Africa, and the nearby Atlantic Islands (Canaries, Madeira, Azores) plotted together as a unit form a zone nearly coinciding with that of *L. emarginatus* (same figure). Eastern Asian material is highly variable, showing in aggregate a zone overlapping most of that of the typical European *niger*, but with most of the measurements falling in an area between the *niger* and *emarginatus* zones. The North American population conforms to the typical European zone. Thus in going from the Atlantic Islands east across Eurasia to North America the scape index alternates high, low, high, low.

The queen scape index is closely correlated. Among six series examined from the Balearics and Canaries, for instance, the SI varied between 77 and 80 and the ML between 0.32 mm. and 0.40 mm. (HW 1.61-1.71 mm.). In twelve series from eastern Asia, the SI varied between 73 and 82 and the ML between 0.21 mm. and 0.27 mm. (HW 1.68-1.78 mm.).

The total distributional data for the appendage character can be condensed as follows. Eight series of workers from several localities in the Canary Islands (Gran Canaria, La Palma, and Teneriffe; W. M. Wheeler leg.; MCZ) fall in the *emarginatus* zone; two (Gran Canaria and Teneriffe) fall intermediate between *emarginatus* and the European *niger*. Three series from San Miguel, Azores (W. M. Wheeler and A. Schatzmayr leg.; MCZ), one specimen from Madeira (MCZ) and four series from several localities in Mallorca and Minorca (W. M. Wheeler and H. Eidmann leg.; MCZ) fall in the *emarginatus* zone. Series

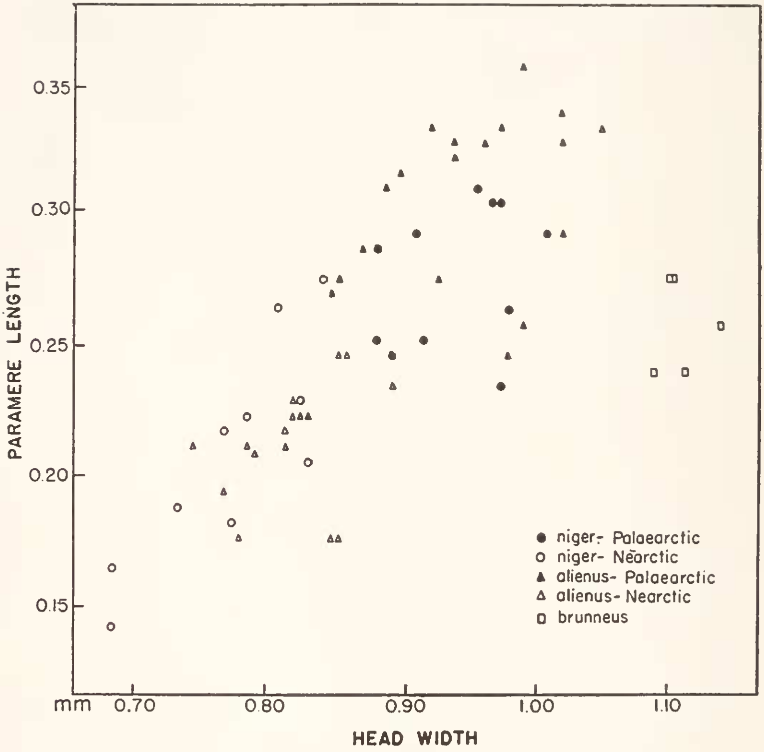

Fig. 7. Head width-paramere length relationships in the male caste of *L. brunneus* and two geographic samples of *L. niger* and *L. alienus*. Further explanation in the text. Nest series chosen at random; no more than two males per series were measured.

from Trolard-Taza, Algeria (Santschi leg.; USNM), and Azrou, Morocco, 1500 meters (Wheeler leg.; MCZ) are in the *emarginatus* zone, while one from Aïn Draham, Algeria (Heyler leg.; Santschi Coll.) is intermediate between *emarginatus* and the European *niger*. Other intermediate records include Centellas, Barcelona, Spain (de Xaxars leg.; MCZ); Lavarone, Venezia Tridentina, Italy (MCZ); Nabresina, Venezia Giulia (Ravasini leg.; MCZ); Mt. Capanne, Elba (Moczarski-Scheerpeltz leg.; MCZ). In general, one gains the impression that this character is clinal, grading away from centers in the Balearics and southern Spain eastward across southern Europe. It is noteworthy that the three series examined from Lebanon (see under distribution) fall in the European *niger* zone.

There is a gap in the data for most of the Middle East and central Asia. The specimen from Naran, Pakistan, previously mentioned falls at the upper extreme of the European *niger* zone, while one series each from Nathagali, Pakistan, and Schirparek, Afghanistan, are well inside the *niger* zone. Within the eastern Asian sample no geographic trend is evident. Series from peripheral localities in western China, Manchuria, and Hokkaido do not depart from the overall population trend toward an intermediate *emarginatus-niger* regression zone.

Male size. As shown in Figure 7, North American males are consistently smaller than those from Eurasia. No geographic trend within the populations of either continent was noted. This geographic pattern is exactly repeated in the closely related species *alienus* (*q. v.*).

Male genitalia. Fifteen males from three nest series from Los Tilos, Gran Canaria, have exceedingly thin parameres, outside the range of variation of the continental population. No other males from the Atlantic Islands have been seen, so that this character cannot be properly evaluated at the present time.

Summary of geographical variation. (1) In Europe the head width-appendage pilosity allometry regression zone of *niger* is well separated from that of its sister species *alienus*. In northeastern Asia and in North America the slope of the zone steepens, and its lower end comes to overlap that of the sympatric populations of *alienus* (Fig. 6). (2) In Formosa the appendage pilosity is denser and more oblique than elsewhere; the same character occurs sporadically throughout the rest of southern and eastern

Asia. (3) Appendage length, as measured by the scape index, exhibits an unusual pattern of alternating polytopic variation; the SI is higher in North Africa, the Balearics, Atlantic Islands (Canaries, Madeira, Azores), and eastern Asia, and lower in Europe and North America. (4) The males are consistently smaller in North America than in Eurasia. (5) The Canary Islands population may show a significant difference in paramere shape, but the data are as yet inconclusive.

DISTRIBUTION (see also Fig. 8). This species has the northernmost range of the four members of the *niger* complex. In Eurasia it is found from Scotland and southern Fennoscandia south to Morocco, Algeria, and the offshore Atlantic Islands, east through Lebanon, Afghanistan, and the Himalayan plateau to central China and Formosa, then north to northern Russia, southern Yakutsk, and Kamchatka. In North America it ranges from the Pacific Northwest through most of the Great Basin, the Rocky Mountains, and northern Sierra Nevada.

According to Donisthorpe (1927), *niger* probably occurs over the entire British Isles, with the possible exception of the northern Scottish islands. O'Rourke (1950) reports that it is common in sandy areas along the Irish coast but is found inland only in the southern half of the country. Holgersen (1944) states that it is common throughout southern Norway, occurring north to Ringebu in central Norway. Forsslund (1947) has found *niger* in Sweden as far north as Lima, Kopparberg. I have seen specimens from Ekenäs, Finland (O. Wellenius leg.; USNM), and Karawajew (1912) reports it as far north as Novgorod in European Russia.

Judging from the abundant material in collections lent to me, the vast number of records in the literature, and the past statements of many European authors, *niger* is very abundant throughout most of central and western Europe. Southward, it is still common in northern Spain from Catalonia to the Basque provinces (published records mostly by Santschi), and has been reported from near Madrid (Santschi, 1931), as well as Soure, in northern Portugal (Santschi, 1932). I have seen material from Centellas, Catalonia (de Xaxars leg.; MCZ); Algeciras, Cádiz (W. M. Wheeler leg.; MCZ); and the Alameda, Gibraltar (Wheeler leg.; MCZ). *Niger* is apparently common on Mallorca and Minorca in the Balearics (records by Eidmann and Łomnicki; collections by Wheeler in the MCZ), and Łomnicki (1925) has recorded it from Santa Eulalia, Ibiza. According to Santschi (1931) this species has been taken in many localities through the middle and high Atlas ranges of Morocco, as well as Kenitra on the Moroccan coast. Verified records for Morocco, Algeria, and the offshore Atlantic Islands have already been given in the section on geographic variation.

Fig. 8. An outline of the known distributions of *L. niger* and *L. alienus* in North America.

Niger probably ranges throughout Italy. I have seen material from Bulach, Sardinia (A. H. Krausse leg.; USNM), and there are literature records for many of the adjacent Tyrrhenian Islands, including Sicily. Zimmermann (1934) gives many records for the Yugoslavian coast, noting that this species is scarce in southern Dalmatia. It is apparently rare in the Near East. I have seen series from the following localities in Lebanon: Hammana, 1100 meters; 2 km. south of Hermel, near the Orontes River, 600 meters; the mountain above the Kammouha Plain, 1900 meters, dealate queens (all K. Christiansen leg.; MCZ).

According to Karawajew (1926, 1927) *niger* has been taken in the Krimea and in many localities in the Caucasus. Kuznetzov-Ugamskij (1929b) found it common in the forests of northern Daghestan and sporadic in the drier southern area. Records verified for Afghanistan, Pakistan, and Soviet Central Asia have already been given in the sections on geographic variation and synonymy. Menozzi (1939) identified a form as "*emeryi*" collected at a number of localities in the Karakoram by the 1929 Duca di Spoleto expedition; this material, destroyed during the war, is probably true *niger* (see under synonymy). There is an excellent chance that *niger* occurs all the way across the southern face of the Himalayas at suitable elevations. Eidmann (1941), in his report on the ants collected by the Brooke Dolan expedition of 1934-35, lists a number of records from the eastern rim of the Tibetan Plateau and the adjacent Hsifan mountain country between 1800 and 3400 meters (localities include Yekundo, Tatsienlu, and Walingpin), and concludes that it is a common species through most of this area.

The following Chinese and Manchurian records have been made during the present revision: Beh Luh Din, Szechwan (D. C. Graham leg.; USNM); Hu Hsien and Miao T'ai Tze, Shensi (W. L. Brown leg.; MCZ); Soochow, Kiangsu (N. G. Gee leg.; MCZ); Nanking, Kiangsu (G. P. Jung leg.; MCZ); Peking, Hopeh (C. F. Wu leg.; MCZ); Tsinghua, Hopeh (Gee leg.; MCZ); Hishika, Manchuria (M. Tomiura leg.; Yasumatsu Coll.); Harbin, Manchuria (Y. Mori leg.; Yasumatsu Coll.). I have examined many series, principally in the Yasumatsu Collection, from over the entire Korean Peninsula; most of these were collected at random by school children, which suggests in itself that the species is abundant in the area. There is also a large number of series in the Yasumatsu and Okamoto Collections and MCZ from Japan, principally from Kyushu, Shikoku, and Honshu, and *niger* must be widespread if not abundant there. It also occurs on the smaller surrounding islands, as shown by the following records (all Yasumatsu Coll.): Amboo, Yakushima (T. Shirozu leg.); Tomioka, Amakusa (Hori and Chô leg.); Tsutsu, Tsushima (Hori and Chô leg.). I have seen three series from Hokkaido (all Yasumatsu Coll.); Nishiashoro (R. Matsuda leg.); Ashoromura (Matsuda leg.); Nayoro (T. Takami leg.). Teranishi (1931) records it from the island of Shikotan, Kuriles. The Formosan records have already been given in the section on geographic variation.

Kuznetzov-Ugamskij (under synonymy) records this species from near Tashkent and Alma Ata, Soviet Central Asia. Holgersen (1943) records it from the Abakan Steppe, Khakass Autonomous Region, and from "Sistikem" (not located), Mongolia. Karawajew (1931) states that it has been found as far north in Siberia as the districts of Tobolsk, Tomsk, Yenisei, and Irkutsk, as well as the Akmolinsk region and Transbaikal. He examined a sizable collection from the remote Yakutsk District and obtained records ranging as far north as Ust-Kut on the Lena River in the west and the junction of the Aldan and Tympton rivers in the east. According to Karawajew also (1912, 1931), *niger* has been taken on Kamchatka and at Mauka and Chappusi on Sakhalin. Kuznetzov-Ugamskij (1929a) found it to be one of the commonest and most widespread ant species in the southern Ussuri region of the Soviet Maritime Territory.

The presence of this species in North America, living sympatrically with *sitkaensis* and *neoniger*, was discovered for the first time during the course of this revision. I have included below records of all of the series which have been examined. WASHINGTON: Blewitt Pass, Kittitas Co. (W. S. Creighton leg. and Coll.). OREGON: Willow Creek Campgrounds, Warner Mts., Lake Co. (B. Malkin leg. and Coll., MCZ). CALIFORNIA: Lake Tahoe (W. M. Wheeler leg.; MCZ). IDAHO: Double Springs Summit, Lost River Range (Creighton leg. and Coll.); Rock Creek Ranger Station, Twin Falls Co., 6400-6800 feet (Malkin leg. and Coll., MCZ); Bloomington Peak, Wasatch Range, Franklin Co., 8500-9000 feet (Malkin leg. and Coll., MCZ). MONTANA: Lake McGregor, Flathead Co. (Creighton leg. and Coll.). COLORADO: Broadmoor, El Paso Co. (MCZ); Cascade, El Paso Co. (MCZ); Manitou Springs, El Paso Co. (W. M. Wheeler leg.; MCZ); Florissant, Teller Co. (2 series, T. D. A. Cockerell and W. M. Wheeler leg.; MCZ); Salida, Chaffee Co. (Wheeler leg.; MCZ). UTAH: Heber, Wasatch Co. (A. W. Grundmann leg.; Cole Coll.); Alta, Salt Lake Co. (Grundman leg.; Cole Coll.); Ogden, Weber Co. (G. F. Knowlton leg.; Cole Coll.); White Canyon, Natural Bridges National Monument, San Juan Co. (C. T. Brues leg.; MCZ). NEW MEXICO: 12 miles east of Taos, Taos Co., 7250 feet (A. C. Cole leg. and Coll.); Ute Park, Colfax Co., 7400 feet (Cole leg. and Coll.); Eagle Nest, Colfax Co., 2 series 8000 and 8600 feet (Cole leg. and Coll.); 2 miles south of Raton Pass, Colfax Co., 7700 feet (Cole leg. and Coll.); Capulin Mountain National Monument, Union Co., 7750 feet (Cole leg. and Coll.); Las Vegas, San Miguel Co., 6400 feet (Cockerell leg.; MCZ); Hayne's Canyon, Sacramento Mts., Otero Co., 8000 feet (Wheeler leg.; MCZ); Willow Creek Ranch, Mogollon Mts., Catron Co., 8300 feet (Cole leg. and Coll.).

ECOLOGY. Gösswald (1932) has presented a detailed and informative account of the habitat preferences and nesting habits of this species in Germany. He found it to be one of the most abundant and adaptable native ants. It occurs in deciduous, coniferous, and mixed forests, along forest borders, in hedgerows, and in open meadows; it thrives on cultivated land and occasionally enters houses. In forests it tends to nest in rotting tree trunks. In exposed situations with little vegetation cover, it nests mostly under stones. In meadows, along grass-grown paths and forest gardens, and in gardens, it frequently builds earthern mounds, especially where the soil is moist and the ground vegetation dense. Such mounds are irregular in shape and apparently designed to surmount the surrounding vegetation, with the result that they are often quite massive and may exceed 50 cm. in height. In a random field sample, Gösswald found 625 nests under stones, 350 in mounds, and 130 in rotting wood. The species is said to occasionally construct carton nests out of macerated plant material and humus, especially when it nests under stones in pine woods; the carton material closely resembles that characteristically manufactured by *L. fuliginosus.*

The North American population shows a similar latitude in habitat preferences. Field notes supplied me with 16 collections by A. C. Cole and Borys Malkin seem to indicate a general preference for drier and more open situations. The majority of the 16 were taken in open forest of variable composition, while several were taken in meadows and grassy roadstrips. One was taken in a dry rabbitbrush association (*Chrysothamnus*) near Eagle Nest, N. Mex. (Cole, see under distribution). Another was taken near timberline in a zone of stunted fir (Bloomington Peak, Wasatch Mts., Idaho; Malkin). The Eagle Nest colony was found in soil at the base of a bush; all of the others were taken under stones.

The previously published Asiatic records seem to indicate broad adaptability also. The Yalung-Yangtse collections recorded by Eidmann (1941) were made both in moist river valleys and in the high grassland of the Tibetan Plateau. All were from under stones. Kuznetzov-Ugamskij (1929a) notes that in the Ussuri region this species occurs under the ''widest environmental conditions.''

Ecological data accompanying several peripheral collections determined during this revision are noteworthy. On the Canary Islands (Gran Canaria, Teneriffe, La Palma) Wheeler (1927) found *niger* mostly in moist, shady spots between 1500 and 5000 feet. At Las Mercedes, Teneriffe (2500 feet), it was the only ant species found in a forest of tree-heath (*Erica arborea*) and laurel (*Cerasus lusitanicus*). At Ponta Delgada in the Azores *niger* occurred abundantly with *Tetramorium caespitum*, nesting under stones and foraging over the ground in files. In Lebanon, Christiansen (*in litt.*) took workers under rocks in mesophytic forest at Hammana and dealate queens from rotting wood in spruce forest above the Kammuoha Plain. Workers were also taken with the aid of a Berlese funnel from around the roots of grass growing on the banks of the Orontes River two miles south of Hermel. This last locality is surrounded by scrub desert and is ten miles from the nearest well developed woodland, representing an extreme habitat record for *Lasius* in general and a very extraordinary one for *niger* in particular.

Niger has generalized food habits. Many authors have observed it gathering insect remains, floral nectar, and the honeydew (excreta) of Homoptera and larval Lycaenidae. Eidmann (1926) and others have suggested that the insect honeydew makes up the bulk of the diet. According to Donisthorpe (1927), in a review of the food habits of this species, *niger* has been observed occasionally to gather seeds of such plants as *Viola, Galium,* and *Ranunculus;* Scott (1926) has seen it collecting seeds of *Chelidonium.* But apparently no one has checked to see if the seeds are actually used as food.

The pastoral habits of *niger* have been the subject of an excellent study by Eidmann (*ibid.*). Certain aphids overwinter in the nests of *niger* and are brought out and placed on the host plants in the spring. At first the aphids are returned to the shelter of the nests each evening. Later, as the nights grow warmer, the herds are left permanently in place. Certain of the workers function as guards (*Wächter*) during the day, remaining constantly at fixed posts; one worker was observed to return to the same spot each day for eight days. The workers appear to reduce predation by the braconid *Trioxys,* and on several occasions Eidmann saw them in the act of driving off workers of other ant species. Büsgen (1891) has observed *niger* workers combating chrysopid larvae in similar fashion. By counting the number of workers returning to the nest gorged with honeydew, Eidmann estimated that a large colony of *niger* may consume as much as a liter of this material in the course of a summer.

According to Eidmann, *niger* is principally nocturnal. Its above-ground activity, as measured by the number of ants soliciting honeydew, is highest at midnight and lowest in the early morning. The workers do all they can to avoid light; in order to work above ground they build turret-shaped shelters around the bases of aphid-infested plants and connect these with the nest by means of covered pathways.

Eidmann (1943) has included this species in a general study of overwintering in ants. Most of the workers of the colony move deep into the center of the nest, concentrating in a few chambers. A small number remain with the aphids in the special chambers where these insects are housed. Brood, in the form of small larvae, may be present or lacking.

According to Donisthorpe (1926), who has undertaken a thorough review of the European literature on the subject, the nuptial flights of *niger* take place in the afternoon and early evening from early July to mid-September. There are no records of nuptial flights in North America, but winged reproductives have been taken *in nido* from July 3 (Sacramento Mts., N. Mex.) to September 1 (Alta, Utah). Stray males and queens, possibly engaged in a nuptial flight, were found at Heber, Utah, on September 7 (A. W. Grundmann). Eidmann (1926) has studied reproduction and nest-founding in this species in Germany. The pair copulate in flight, fall to the ground, and separate. The queen, without attempting to take flight again, soon drops her wings and seeks cover. The first eggs are laid the following spring, and the first adult brood hatches that summer. One queen was observed to go without food for 382 days in the normal course of founding a colony.

SYNONYMY. *Lasius niger* var. *alieno-niger* Forel. True hybrids between the European populations of *niger* and *alienus* must be very rare or non-existent. Taking into account the strong allometry shown by both species in the chief diagnostic character, I have failed to find a single European nest series which I could call an interspecific hybrid (Fig. 6). The series determined as *alieno-niger* in the MCZ (including the Finzi Collection) have invariably turned out to be small *niger* workers. But even if true hybrids were to be found eventually, and these included the *alieno-niger* types, the name definitely implies a special hybrid origin and cannot be used under the recent revisions of the International Rules of Zoological Nomenclature (Hemming, 1953).

Lasius niger flavescens Forel. Lectotype by present selection, a worker in the AMNH. Pronotum crushed on right side, HW 0.86 mm., SL 0.87, SI 101, seta count 37. This specimen has an unusual body coloration, a light yellowish brown of the shade typical of *L. umbratus.* It also has unusually abundant body hair, 27 standing hairs projecting beyond the thoracic border and 18 beyond the propodeal border when the alitrunk is seen in side view, but this is still within the extreme limits of normal *niger* variation. In suggesting synonymy in this case, I do not discount the remote possibility that *flavescens* may eventually be shown to represent a distinct Central Asian sibling of *niger.*

Lasius niger emeryi Ruzsky. The principal characters offered by Ruzsky are paler color (reddish yellow alitrunk) and short oblique hairs on the scapes and tibiae. The hairs are sparser on the scapes than on the tibiae and presumably overall sparser than in the typical *niger.* I believe that this form represents an intermediate to the geographic variant already described as characterizing Formosa and ranging west to Pakistan. In fact, a specimen judged as such from Nathagali, N. W. F. P. (Weber Coll.), not far from the *emeryi* type locality, agrees well with Ruzsky's description except for a darker body coloration.

Kuznetzov-Ugamskij's *Acanthomyops niger nitidus, A. niger alienus* var. *pilicornis*, and *A. niger* var. *minimus* were described as trivial variants of *niger*. *Nitidus* was characterized as having a more shining sculpture and *pilicornis* as having scattered oblique hairs (see under geographic variation for this character), while *minimus* was distinguished only by smaller size. All three seem well within the normal variation of *niger*.

Lasius emarginatus var. *nigrescens* Stitz. Lectotype by present selection, a queen in the Berlin Museum. HW 1.51 mm., SL 1.28 mm., SI 85, ML 0.19 mm., thorax width anterior to tegulae 1.87 mm. Eight syntopotype queens from the same collection were also examined. The type series is typical *niger* in pilosity, color, and alitruncal profile. The SI is at the upper extreme obtained in measurements of ten series of *niger* from eastern Asia, but the ML is below the range of the same series (and of *emarginatus*) and well within the range of the European *niger*. There is no evidence that *emarginatus* occurs this far east.

Lasius niger coloratus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.71 mm., HW 1.04 mm., SL 1.07 mm., SI 103, ML 0.20 mm., EW 0.20 mm. One other syntype worker examined. These two specimens are typical of the Formosan pilosity variant described in the section on geographic variation.

Lasius emarginatus var. *japonicus* Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.62 mm., HW 0.96 mm., SL 0.98 mm., SI 102, ML 0.20 mm., EW 0.19 mm., seta count 21. One other syntype worker examined. These specimens are typical *niger*, conforming to the general trend in the eastern Asiatic population by having appendage length in a zone intermediate between *niger* and *emarginatus*. The appendage pilosity seems to be somewhat diminished, but it is impossible to tell with certainty whether it fits the regression zone typifying northeastern Asia.

Lasius transylvanica Röszler. Prof. Röszler (*in litt.*) has informed me that the types of this specimen are at present unavailable to him and may have been destroyed during the Second World War. The species is supposed to be close to *niger,* differing by having hairless tibiae associated with normally hairy scapes. It is said to be peculiarly adapted to living in the vicinity of water on the floodplain of the Nyárad River and to show corresponding behavioral differences. It is my personal opinion that Röszler at the most was observing ordinary *niger* under exceptional ecological conditions and that the morphological characters may have been unduly exaggerated. I think the most practical course at the present time would be to place *transylvanica* in the provisional synonymy of *niger* to await the day that Röszler's observations can be repeated.

Lasius alienus (Foerster)
(Subg. *Lasius*)

Formica aliena Foerster, 1850, Hymenopterologische Studien (Ernst Ter Meer Publ., Aachen), **1:** 36–38; worker, male; original description. Type locality: Lousberg; a suburb of Aachen, Germany.

Prenolepis lasioides Emery, 1869, Ann. Accad. Natur. Napoli, **2:** 6–7; pl. 1, figs. 3, 3A; worker, queen, male; original description. Type locality: Naples, Italy. NEW SYNONYMY.

Lasius niger var. *lasioides,* Ruzsky, 1905, Formicariae Imperii Rossici, p. 310.

Formicina nigra lasioides, Emery, 1916, Bull. Soc. Ent. Ital., **47:** 177.

Lasius alienus lasioides. Zimmermann, 1934, Verh. Zool.-bot. Ges. Wien, **84:** 49.

Prenolepis fuscula Emery, 1869, Ann. Accad. Natur. Napoli, **2:** 8; worker; original description.

Lasius fumatus Emery, 1870, Bull. Soc. Ent. Ital., **2:** 194. *Nomen pro Prenolepis lasioides.*

Lasius niger alienus, Forel, 1874, Les Fourmis de la Suisse, p. 46.

Formica pallitarsus Provancher, 1881, Canadian Naturalist, **12:** 355–356. Synonymy by André, 1887, Revue d'Ent., p. 288.

Lasius niger var. *americanus* Emery, 1893, Zool. Jahrb. Syst., **7:** 639; worker, queen, male; original description. Type locality: Virginia, by present restriction. NEW SYNONYMY.

Lasius americanus, E. Gregg, 1945, Ann. Ent. Soc. Amer., **38:** 530.

Lasius alienus americanus, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 419.

Lasius niger var. *grandis* Forel, 1909, Ann. Soc. Ent. Belg., **53:** 104–105; worker; original description. Type locality: Ronda, Malaga, Spain. NEW SYNONYMY.

Lasius niger alienus var. *alieno-americanus* Wheeler, 1917, Proc. Amer. Acad. Arts Sci., Boston, **52:** 525–526; queen; original description. Type localitly: Banff, Alberta; by present restriction. NEW SYNONYMY.

Lasius niger turcicus Santschi, 1921, Bol. Soc. Esp. Hist. Nat., **21:** 115–116; worker, *nec* queen; original description. Type locality: Ankara, Turkey. NEW SYNONYMY.

Lasius niger lasioides var. *barbara* Santschi, 1921, ibid., p. 170; worker, original description. Type locality: Sidi Aïch, Tunisia. NEW SYNONYMY.

Lasius brunneus var. *barbara* Santschi, 1936, Bull. Soc. Sci. Nat. Maroc, **16:** 208.

Acanthomyops niger alienus var. *flavidus* Kuznetzov-Ugamskij, 1927, Rev. Russ. Ent., **21:** 189; worker; original description. Type locality: Dzhungarski Ala Tau Mountains, Alma Ata, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger alienus var. *turkmenus* Kuznetzov-Ugamskij, 1927, *ibid.*, p. 189; worker; original description. Type locality: Geok Tepe, Turkmen S. S. R., Soviet Central Asia. NEW SYNONYMY.

Lasius brunneus var. *obscurata* Stitz, 1930, Mitt. Zool. Mus. Berlin, **16:** 239–240; worker, queen; original description. Type locality: Dschailgan, Karateghin, western Pamirs, Tadzhik S. S. R., Soviet Central Asia, 1800 meters. NEW SYNONYMY.

Lasius alienus illyricus, Zimmermann, 1934, Verh. Zool.-bot. Ges. Wien., **84:** 50–52; worker, queen, male; original description. Type locality: Dubrovnik, Yugoslavia. NEW SYNONYMY.

Lasius alienus var. *pannonica* Röszler, 1942, Siebenbürgischer Ver. Naturw., Hermannstadt, Verh. und Mitt., **91-92:** 40; worker, queen; original description. Type locality: not designated. NEW SYNONYMY.

Lasius alienus var. *pontica* Stärcke, 1944, Ent. Ber., **11:** 156–157; worker; original description. Type locality: Neu Athos (Nowyi Afron), Caucasus, Georgian S. S. R. NEW SYNONYMY.

DIAGNOSIS. All three castes are extremely close to *niger*. The only character found to be of consistent diagnostic value is quantity of appendage pilosity, described in detail below.

Worker. Within the PW range of 0.53-0.70 mm., the seta count is always less than 20 and usually less than 10. The seta count is strongly allometric, making it advisable to determine individual specimens by comparing them with the regression zones of Figure 6. In Europe the regression zones of *niger* and *alienus* are parallel but well segregated; the *alienus* line is set so that the great majority of workers have seta counts of less than 5, while most *niger* exceed 20. In eastern Asia, on the other hand, *alienus* evidently becomes scarcer, and the *niger* zone shifts down and forward to become contiguous with that of *alienus*. As a result, a small number of individuals cannot be safely determined to either species.

Queen. Seta count never exceeding 10 and usually 0.

Male. Seta count almost always 0.

TYPES. Dr. H. Bischoff has informed me that no syntypes of *alienus* can be located in the Foerster Collection in the Berlin Museum. What may be part of the type series has been found instead in the Mayr Collection and lent me by Dr. M. Beier. This consists of two pins, one holding two workers and the other a single male, labelled "Aach. Först/Las. alienus det. Mayr." The workers are identifiable as typical *alienus*.

FURTHER DESCRIPTION. *Worker.* Size ranging and averaging smaller than in *niger*. In a sample of 147, with no more than 2 per nest series, mean with standard error 0.56 ± 0.004 mm., standard deviation 0.054 mm. Color averaging lighter than *niger*, although total variation in both species shows complete overlap.

Queen. Size averaging smaller than *niger* when the North American populations are included.

Males. Size range about the same as in *niger* and showing parallel geographic variation. Mandibles typically of *niger* type, but in two series (Engadin, Switzerland, Kutter leg. and Coll.; Hornet, Beltrami Co., Minn., A. Achenbach leg., G. C. Wheeler Coll.) the mandible type is closer to the intermediate type already described for *L. brunneus*. Subgenital plate showing the same wide variation as in *niger;* series from Godinne, Belgium (A. Raignier leg.; MCZ) and the Engadin Valley, Switzerland (Kutter) encompass within themselves the full variation from the unilobed to bilobed condition.

GEOGRAPHIC VARIATION. Two significant independent trends have been noted in *alienus* and are described in detail below.

(1) The entire North American population appears to be separable as a unit from the Eurasian on the basis of male size (Fig. 7). Despite a strong partition between the two populations, it will be noted that both fall along the same HW-paramere length regression zone, and some overlap in individual measurements exists, so that the two populations cannot be

considered as distinct species on the basis of male size alone. No clinal trend within either population was noted. Correlated with this morphological character is a striking ecological difference, to be treated in some detail later. *Alienus* males from eastern Asia were not available during the present study.

(2) In the area encompassing the Balkans and northwestern Iran, appendages are often elongated as in the related species *emarginatus*. During the present study *alienus* with scape indices in the *emarginatus* regression zone (Fig. 5) have been recorded from the following localities: Dubrovnik, Yugoslavia (*illyricus* Zimmermann syntypes); Cetinje, Yugoslavia (Kutter Coll. and MCZ); Karlovo, Bulgaria (J. H. Kendall leg.; MCZ); Caspian, northwestern Iran (P. A. Buxton leg.; Oxford University Museum). An intermediate condition occurs in series from Lushnja, Albania (MCZ); Ankara, Turkey (*turcicus* Santschi syntypes); and Talysch District, Azerbaijan S. S. R. (MCZ). The character may also occur in Stärcke's var. *pontica* from Neu Athos, Georgian S. S. R. (see under synonymy). It may predominate in central and southern Yugoslavia, judging from the rather limited number of series examined from there, but it is less common or absent in adjacent areas. Numerous series from Bulgaria, Albania, the Istria-Cherso region, and northeast Italy, along with a few others from Greece, Lebanon, Turkey, Iraq, and Georgian S. S. R. all fit in the *alienus* regression zone. Farther east, a series from Srinigar, Kashmir (full citations for this and the following records are given in the next section) appears to fall between the *brunneus* and *alienus* zones, but the workers are too small to afford exact placement, since *brunneus* minimas of comparable size have not been available. A single worker from the Duany Tau Mountains, Kazakh S. S. R., falls in the upper *alienus* zone. The type series of Stitz's "*brunneus* var. *obscurata*", from the western Pamirs, falls in the middle of the *alienus* zone. Series from Kunming, China; Harbin, Manchuria, and Seoul, Korea, are well within the *alienus* zone. The entire North American population also falls within the *alienus* zone.

The appendage elongation trend in the Balkans is significant on two counts. First, *alienus* tends to converge toward *emarginatus* in the appendage character in the same area where *emarginatus* converges toward *alienus* in color. As a result, two of the important differences which separate these species over most of their ranges are lost. Second, *alienus* copies in this area a trend taken by *niger* over much of its own range. But where *alienus* occurs in North Africa and eastern Asia, it does not follow *niger*, while *niger* in turn fails to follow it in the Balkans.

DISTRIBUTION (see also Fig. 8). *Alienus* has the widest distribution of all the members of the genus. In Eurasia it is found from the British Isles and southern Fennoscandia south to Morocco-Tunisia, east through Lebanon and Iraq to Kashmir and southern China, and north into European Russia, central Asia, China, and Japan. Unlike *niger*, it apparently does not occur in the Balearics, Canaries, and Azores, or in Formosa. In North America it is found from southern British Columbia to Nova Scotia and south to the mountains of Durango, Mexico, in the west, and to northern Florida in the east.

In England, according to Donisthorpe (1926), *alienus* is less common than *niger* and has been collected northward only to the central counties of Suffolk and Oxford. O'Rourke (1950) finds it scarce but widespread in Ireland. Stitz (in Strand, 1912) gives two records from southern Norway, but Holgersen (1944) in an extensive faunal study failed to find it in that country. I have seen two collections from southern Finland: Lappvik (O. Wellenius leg.; USNM), and Metsäpirti (Forsius leg.; MCZ). Ecological and local faunal studies by a number of European authorities indicate that *alienus* is subordinate to *niger* in most of northern and central Europe but is more prominent along the Mediterranean coast. It occurs sporadically through Spain, being recorded from the provinces of Catalonia and La Mancha by Menozzi (1932). I have verified the following two North African records: Biskra, Algeria (Stauder leg.; MCZ); Sidi Aïch, Tunisia (var. *barbara* Santschi syntypes). I have determined material from over most of Italy and a single series from Sorgono, Sardinia (A. H. Krausse leg.; MCZ). Several authors, particularly Emery (1915), have recorded it from the islands of Palmaria, Elba, Giglio, Asinara, and Sicily. I have seen series from many localities through Yugoslavia and Albania. It probably occurs over most of Greece; I have seen material from as far south as Andros Island, in the Cyclades (F. Werner leg.; MCZ). Forel (1911) records it from Athens, Menozzi (1928) records it from the Dodecanese, and Emery (1894) records it from Crete.

Since the Asiatic population is very hard to distinguish from the sympatric *niger* population and published records are manifestly unreliable, I have presented in the list below all records verified during the present study. Near East records are also included here for convenience.

TURKEY: Istanbul (K. Christiansen leg.; MCZ); Ankara (*turcicus* Santschi syntypes); Kars (C. Kosswig leg. and Coll., MCZ). LEBANON: mountain above the Kammouha Plain, 3 series at 1500 meters and 3 at 1800 meters (Christiansen leg.; MCZ). IRAQ: Shaglawa, near Ruwandiz (N. Weber leg. and Coll., MCZ). IRAN: northwest Iran, near the Caspian Sea (Buxton leg.; Oxford University Museum). U. S. S. R.: Krimea (W. Karawajew leg.; MCZ); Talysch District, Azerbajian S. S. R. (MCZ); Tiflis, Georgian S. S. R. (MCZ); Duany Tau Mountains, Kazakh S. S. R. (N. Kusnezov leg.; MCZ). KASHMIR: Srinigar (R. K. Enders leg.; Weber Coll. and MCZ). CHINA: Kunming, Yunnan Prov. (F. Silvestri leg.; MCZ). MANCHURIA: Harbin (Y. Mori leg.; Yasumatsu Coll.). JAPAN: Towada, Honshu (Esaki and Yasumatsu leg.; Yasumatsu Coll.).

For reasons already presented, literature records from Asia must be treated with extreme caution. I have noted the following which are of possible significance in extending the range as documented above: Ashkabad, Turkmen S. S. R. (Forel, 1903); Geok Tepe, Turkmen S. S. R. (var. *turkmenus* Kuznetzov-Ugamskij); southern Mongolia (Stitz, 1934). A record by Forel (1913) from Ceylon is of course highly dubious. The scarcity of records in the many Asian faunal lists published in the past tends to support my own conclusion that *alienus* is much less common there than *niger*.

In eastern North America, *alienus* is abundant from southeastern Canada to the southern Appalachians. The northernmost record known to me is Pleasantfield, Nova Scotia (W. H. Prest leg.; MCZ). I found the species abundant in Massachusetts and southern Ontario (Plantagenet, Ottawa, Sturgeon Falls, Deux Rivieres, Blind River), while large random collections by Mary Talbot in Livingston Co., Mich., and by Kenneth Kraft in Itasca State Park, Minn., establish the fact that it is generally abundant at this latitude. Collections by A. C. Cole and myself in the Appalachians of North Carolina and Tennessee show it to be common there at intermediate elevations up to 5100 feet and ranging as high as 5800 feet (peak of Grandfather Mt., N. C.). It has been taken as far south as northern Florida, but is rare and locally distributed in the Gulf States. I have verified only the following records from this area.

GEORGIA: Mosquito Creek, Decatur Co. (P. B. Kannowski leg.; UMMZ and MCZ). FLORIDA: 6 miles south of Chattahoochee, Gadsen Co. (Kannowski leg.; UMMZ and MCZ); ''Camp Torreya'', Liberty Co. (T. H. Hubbell leg.; UMMZ); Monticello, Jefferson Co. (MCZ); Gainesville, Alachua Co., a single alate queen (MCZ). ALABAMA: Decatur, Morgan Co. (E. O. Wilson leg.; MCZ); Tuscaloosa (Wilson leg.; MCZ); Chunchula, Mobile Co. (Wilson leg.; MCZ); Phillipsville, Baldwin Co. (Wilson leg.; MCZ); Pollard, Escambia Co. (Wilson leg.; MCZ); Brewton, Escambia Co. (Wilson leg.; MCZ); Ariton, Dale Co. (Wilson leg.; MCZ); Blue Springs, Barbour Co. (Wilson leg.; MCZ); Chattahoochee State Park, Houston Co. (Wilson leg.; MCZ). MISSISSIPPI: no further data (USNM).

In the north-central states, *alienus* is abundant west to the limit of the deciduous forest. Judging from the exhaustive collections made by G. C. Wheeler and his students, it is one of the several dominant species of the genus in eastern North Dakota, but declines rapidly in the deciduous forest-grassland transition belt and is sporadic in the nearly treeless western half of the state. It is present but uncommon in the northern Rockies, being known only from the several following records. MONTANA: 2 miles east of Kiowa, Glacier Co. (E. O. Wilson leg.; MCZ); St. Marys, Glacier Co. (Wilson leg.; MCZ); Browning, Glacier Co. (W. S. Creighton leg. and Coll.); Fish Creek, Glacier Nat. Park (Creighton leg. and Coll.). IDAHO: North Fork, Lemhi Co. (Creighton leg. and Coll.).

Alienus must be sparse or absent in the southern Rockies and Great Basin; no records have been forthcoming from the large collections made there by Cole, Creighton, and Grundmann. It is widespread in the mountains of southern Arizona, as indicated by the following records: Rustler Park, Chiricahua Mts. (B. Malkin leg. and Coll., MCZ; and Creighton leg. and Coll.); Ramsey Canyon, Huachuca Mts. (Creighton leg. and Coll.); Stratton, Santa Catalina Mts. (W. M. Wheeler leg.; MCZ); Wet Canyon, Graham Mt. (Malkin leg. and Coll., MCZ). I have seen one extraordinary collection from 32 miles west of El Salto, in the Sierra Madre Occidental of southern Durango, at 8700 feet (Creighton leg. and Coll., MCZ). There is an excellent possibility that the species is widely distributed at suitable elevations in other parts of northern Mexico.

Going northward along the Pacific coast, *alienus* has been encountered at Donomore Meadows in the Siskiyou Mountains of northern California, at 5600 feet (Creighton leg. and Coll.). North of this locality, it is apparently common through Oregon and Washington to southern British Columbia. OREGON: La Grande, Union Co. (Cole leg. and Coll.); Pistol River, Curry Co. (Malkin leg. and Coll., MCZ); Brookings, Curry Co. (Malkin leg. and Coll., MCZ); Portland (MCZ). WASHINGTON: Pullman (W. M. Mann leg.; MCZ); San Juan Island (T. Kincaid leg., Cole Coll.; Mann leg., MCZ). BRITISH COLUMBIA: Royal Oak, V. I. (MCZ); Lillooet (MCZ); Emerald Lake (W. M. Wheeler leg.; MCZ).

ECOLOGY. The Eurasian and North American populations differ markedly from one another in habitat preference. In North Africa and France (Bernard, 1950; Scherdlin, 1909), Ireland (O'Rourke, 1950), England (Diver, 1940), Germany (Gösswald, 1932), East Prussia (Skwarra, 1929), and Daghestan (Kuznetzov-Ugamskij, 1929), *alienus* typically inhabits open dry situations, nesting under stones and occasionally constructing crater entrances in open soil. It shows much less latitude in nesting sites than its sister species *niger*, but is more successful in cultivated areas. Bernard notes that in France it is able to replace *niger* entirely in pastures, even at high elevations, but tends to give way in turn to *Tapinoma simrothi* and *T. nigerrimum*. Diver, in an intensive study of the comparative ecology of *alienus* and *niger* in a local area in Dorset, found *alienus* restricted mostly to dry heath, whereas *niger* occurred in every major habitat studied. In Daghestan, Kutznezov-Ugamskij found *alienus* to have more southern affinities than *niger*. Where the two occur together, *alienus* is limited mostly to the steppes and mountain meadows (up to 11,000 feet), while *niger* occurs mostly in the forests.

In North America *alienus* reverses this habitat preference. Over its entire range on this continent, it shows a strong predilection for well shaded woodland, where it nests in rotting logs and stumps and under stones. Among the hundreds of colonies I have encountered in the field in the eastern United States, nearly all conformed to this ecological character. It may happen, however, that at high elevations or at the northern periphery of its range, the species occasionally nests in open situations. At the summit of Grandfather Mountain in North Carolina, for instance, I found a small but vigorous population living under stones in an open blueberry-and-heath "bald". The elevation was 5800 feet, higher by 700 feet than any other collection of the genus made in the course of several field trips in the southern Appalachians.

I would like to venture the suggestion that the difference in habitat preferences between the Eurasian and North American populations may be a reflection of competition with various other members of the genus. In Eurasia *alienus* is replaced in most habitats, including woodland, by its extremely successful and abundant sister species *niger*. In North America it is replaced in nearly every available habitat except woodland by the equally successful and abundant members of the *neoniger* complex. As previously indicated in the description of the ecology of that species, *sitkaensis* occupies the same types of nesting sites as *alienus* and probably limits its northward spread. In general, one gains the impression that in Eurasia and North America *alienus* has been squeezed into relatively narrow ecological ranges by its congeneric competitors, but is nevertheless eminently successful within those ranges.

Alienus probably does not differ much from *niger* in food habits and ethology. Several Europeans, including Gösswald (*ibid.*) and O'Rourke (*ibid.*) have independently observed that *alienus* tends to be the more secretive of the two species. This is possibly correlated with the preference of this species in Eurasia for more exposed situations.

Records of nuptial flights in this species are too sparse to allow a rigorous comparison with *niger*. In Europe winged forms are found *in nido* during about the same period as for *niger*. I have records ranging from June (Trieste, MCZ; no further date) to October 28 (Italy, MCZ) without evident preponderance during any part of this period; a single pair were preserved in copula in October (Trieste; MCZ; no further date). In North America records range from May 30 (Decatur

Co., Ga.) to December 4 (Alachua Co., Fla.). Both of these are very exceptional dates, however; the majority of the other records fall in August.

SYNONYMY. *Prenolepis lasioides* Emery. Lectotype by present selection, a queen in the Mayr Collection. HW 1.43 mm., HL 1.26 mm., SL 1.10 mm., SI 77, seta count 0. One worker and one male syntype in the same collection also examined. Worker PW 0.38 mm., HW 0.57 mm., SL 0.67 mm., SI 123, seta count 0. Male HW 0.67 mm., paramere length 0.17 mm. With the possible exception of size and wing infuscation, the lectotype conforms precisely to *alienus* in every character. I have not seen other Palaearctic *alienus* this small but possess series from North America ranging to an even smaller size (e.g. Middlesex Fells, Mass.; W. L. Brown leg.; MCZ). The wings are more infuscated than usual but still within the range of normal variability of at least the North American population. The worker syntype is also exceptionally small, about the size of ordinary *alienus* nanitics, and does not differ from these nanitics in any character. Workers determined as *lasioides* by Forel (AMNH), Santschi (Santschi Coll.), and Finzi (MCZ) have also proven to be nothing more than small *alienus*. Differences quoted by various other authorities such as Zimmermann and Stärcke involve decrease of body hair and attenuation of body form, both purely allometric characters showing an even gradation from the largest workers of the "var. *grandis*" class to the smallest of the *lasioides* class. Finally, the male syntype is very small but otherwise a typical *alienus*.

Lasius niger var. *americanus* Emery. Lectotype by present selection, a worker in the Emery Collection labelled "Va. July 1, 85." PW 0.62 mm., HW 0.92 mm., SL 0.89 mm., SI 97, ML 0.17 mm., EW 0.18 mm., seta count 0. Two syntype workers and three syntype queens were also examined. All are typical *alienus*. As pointed out previously, the North American population can be separated as a unit from the Eurasian population on the basis of male size and will pass conventional subspecies requirements. My reasons for not employing trinomens in this and other such cases have already been explained in the introduction. If future myrmecologists for some reason choose to use this particular trinomen, however, they should bear in mind that Provancher's name *pallitarsus* has precedence, and *ameri-*

canus should be held in abeyance until its status as a *nomen conservandum* has been asserted (see "Principal of Conservation" in *Copenhagen Decisions on Zoological Nomenclature,* Hemming, 1953).

Lasius niger var. *grandis* Forel. Lectotype by present selection, a worker in the Forel Collection. PW 0.87 mm., HW 1.25 mm., SL 1.18 mm., SI 94, ML 0.21 mm., EW 0.24 mm., seta count 26. Syntype workers: PW 0.69 mm. and seta count 16; PW 0.69 mm. and seta count 19. The seta counts of these exceptionally large specimens place them in the *alienus* allometry regression zone; *niger* workers of comparable size have seta counts between 40 and 70. It is impossible to say whether *grandis* represents a geographic variant, since no other material from southern Spain has been forthcoming. North African series taken nearby are about average in size for the species.

Lasius niger alienus var. *alieno-americanus* Wheeler. This variety was created by Wheeler in a singularly haphazard way. In describing "*americanus*" from western North America, he actually had before him four species, *alienus* (Foerster), *crypticus* Wilson, *sitiens* Wilson, and *sitkaensis* Pergande. He noted that some of the queens in this material had longer wings and, erroneously assuming this to be a character of the European *alienus,* proposed his intermediate varietal name for them. Since he failed to designate types, there is no way to tell exactly which of the series of "*americanus*" he had in mind. I have designated the Banff, Alberta, series of *alienus* as a ceremonial procedure to formally dispose of the name. This series is typical for the species in every respect, while the males are of the size characteristic of the North American population.

Lasius niger turcicus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.53 mm., HW 0.76 mm., SL 0.80 mm., SI 105, ML 0.16 mm., EW 0.17 mm., seta count 0. The single syntype queen was also examined. The lectotype is typical *alienus* in every character except for the geographic appendage character discussed previously and a more abundant body pilosity: seen in full face, two standing hairs extend beyond the right genal margin, and three beyond the left margin (typical *alienus* has, at most, one to a side). That this slight pilosity difference is not of species significance is suggested by the fact that a single series from Kammouha, Lebanon (Christiansen) shows completely linking variation; and that it does not have special geographic significance is indicated by the fact that a series from Kars, Turkey (Kosswig) has a typical *alienus* pilosity. Apparently the main reason Santschi described *turcicus* was that he considered the syntype queen, supposedly associated with the lectotype worker, to be markedly different in proportion-characters from the typical *Lasius niger.* I am forced to agree with him fully, since the queen upon examination has proven to be not a *Lasius* at all, but *Prenolepis nitens* Mayr.

Lasius niger lasioides var. *barbara* Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.53 mm., HW 0.81 mm., SL 0.78 mm., SI 96, ML 0.15 mm., EW 0.18 mm., seta count 0. Three syntype workers also examined. That Santschi was able casually to jumble "*lasioides*" (=*alienus*) and *niger* together to form a mount for *barbara* and later to place this form under *brunneus* is both a fair indication of how little he knew about the genus in which he was prolifically describing new forms, and an illustration of the inane nomenclatural arrangements so often employed as a matter of course in ant taxonomy. The *barbara* types are somewhat darker and shinier than the average European *alienus,* but well within the range of normal variation of the species.

Kuznetzov-Ugamskij's *Acanthomyops niger alienus* var. *flavidus* and *A. niger alienus* var. *turkmenus* were described as nothing more than color and pubescence varieties of *alienus.* Both are evidently well within the range of normal variation of the species.

Lasius brunneus var. *obscurata* Stitz. Lectotype by present selection, a worker in the Berlin Museum. PW 0.59 mm., HW 0.90 mm., SL 0.92 mm., SI 102, ML 0.18 mm., EW 0.19 mm., seta count 0. Four syntype workers and the syntype queen also examined. The queen SI is unusually high (SI 80; HW 1.61 mm.), and both castes have unusually sparse body pilosity. Otherwise the series is typical *alienus.*

Lasius alienus illyricus Zimmermann. Lectotype by present selection, a worker in the MCZ from a series labelled "no. 532, Ragusa = Dubrovnik, Mte. Petka, Erdnest, Mai 1928, in Alkohol." PW 0.57 mm., HW 0.84 mm., SL 0.93 mm., SI 110, ML 0.20 mm., EW 0.19 mm., seta count 3. Ten other synnidotype workers examined. This series is typical of *alienus* except for elongated appendages (see under geographic variation). The character in tibial pilosity emphasized by Zimmermann is not sufficient to distinguish this series from the European population.

Lasius alienus var. *pannonica* Röszler. The original description of the worker (*fide* Stärcke, 1944) contains practically nothing of diagnostic value. The queen, on the other hand, is stated to be smaller, more slender, and completely lacking pilosity. Since the whereabouts of the types are unknown (Röszler, *in litt.*), synonymy in this case is only conjectural and based on the assumption that the workers do not differ in actuality from typical *alienus*. There is an excellent possibility that the queen belongs to another formicine or dolichoderine genus.

Lasius alienus var. *pontica* Stärcke. The principal diagnostic character given for the type series, chosen from the type series of *alieno-brunneus* Forel after a lectotype for that variety had been selected, is the greater length of the scapes. This seems to be consistent with the trend already noted (under geographic variation) for the Balkans-Iranian population, and of which Zimmermann's prior form *illyricus* is a good example. Other characters in color, head shape, etc., given to distinguish *pontica* do not appear to be of taxonomic consequence when variation in the entire European population is taken into account.

LASIUS EMARGINATUS (Olivier)

(Subg. *Lasius*)

Formica emarginata Olivier, 1791, Encycl. Method. Insect., **6**: 494; queen; original description.

Lasius emarginatus, Mayr, 1861, Die europäischen Formiciden (Carl. Gerold's Sohn), p. 49.

Lasius niger emarginatus, Forel, 1874, Les fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 46.

Lasius niger nigro-emarginatus Forel, 1874, *ibid.*, pp. 47, 49; worker, female; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger brunneo-emarginatus Forel, 1874, *ibid.*, p. 47; worker; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger emarginatus var. *brunneoïdes* Forel, 1874, *ibid.*, p. 47. NEW SYNONYMY (objective synonym of *brunneo-emarginatus* Forel).

DIAGNOSIS. As a member of the close-knit and difficult *niger* complex, *emarginatus,* like *niger,* must be determined by careful examination of multiple characters. It is easily separable from *niger* and *alienus* over part of its range on the basis of color and appendage length, but the three species tend to show convergent variation in the Balkans area, Mediterranean perimeter, and southcentral and eastern Asia.

Worker. (1) Scape and other appendages longer relative to body size than in all other members of the genus except *productus* Wilson. Eliminating the largest workers (HW 1.10 mm. or greater), the SI exceeds 103 in more than 95 per cent of nest series examined (Fig. 5); 95 per cent or more of *niger* and *alienus* in the same size range have an SI of less than 103, with the following exceptions: *niger* from the Balearics, North Africa, Canaries, and eastern Asia; and *alienus* from the Balkans and eastern Asia.

(2) As a corollary of (1), ML exceeding EW.

(3) Thoracic dorsum low and flattened with respect to the propodeum; if the heights of the propodeum and mesonotum are measured in profile from a base line drawn from the lowest point of the prosternum (anterior to the coxal insertion) to the lowest point of the mesosternum, the propodeum is *usually* about 1.05 × higher than the mesonotum; the two points are usually of equal height in *niger* and *alienus.*

(4) Scape with abundant standing hairs predominantly or entirely subdecumbent and tending to be concentrated on the distal third (Pl. 1, Fig. 8). Rarely the standing hairs may be predominantly suberect-erect or altogether lacking (see under further description below). *Niger,* especially from eastern Asia, occasionally approaches this typical *emarginatus* condition.

(5) Coloration of medium and large workers (i.e. workers with PW about 0.53 mm. or greater) usually distinctive. Alitrunk and petiole yellowish red, contrasting with both the head, which is medium to dark brownish red, and the gaster, which is dark brownish red. The alitrunk and petiole occasionally darken to approach the *niger-alienus* coloration; this divergent condition appears to preponderate in the Balkans population.

Queen. (1) Within a HW range of 1.61-1.70 mm. in a limited number of series measured, SI ranged 76-86. If this is a general condition it allows a 90 per cent separation from sympatric series of *niger,* exclusive of the southern European and North African populations previously described.

(2) ML in this sample ranged 0.23-0.26 mm.

(3) Scape densely clothed with preponderantly subdecumbent and occasional decumbent hairs one-third to one-half as long as the maximum scape width.

(4) Alitrunk medium reddish brown, the head and gaster somewhat darker and tending to contrast against the alitrunk, but never so much as in the worker. This same coloration is closely approached by callow *niger* queens, so that separation on this character alone is difficult.

Male. (1) Within a HW range of 0.92-1.07 mm. in a limited number of series measured, SI ranged 70-76.

(2) ML in this sample ranged 0.24-0.28 mm.

(3) Scape with numerous decumbent hairs one-fourth to one-half as long as the maximum scape width, and few or no suberect or erect hairs.

(4) Subgenital plate typically similar in outline to that of *L. sitkaensis,* but larger (in five nest series measured, maximum transverse length ranged 0.59-0.73 mm.), and more arc-shaped: the posterior border tends to be evenly concave, sweeping back evenly to the prominent posterolateral flanges, while the anterior border is correspondingly convex (one exception noted, see further description below).

FURTHER DESCRIPTION. *Worker.* In a sample of 75, with no more than 2 per nest series, PW range 0.48-0.78 mm., mean with standard error 0.633 ± 0.006 mm., standard deviation 0.050 mm. Total range of SI 103-122, a strongly allometric character with highest values in the minimas. Head tends to be narrower than in *niger* and *alienus*, but considerable overlap occurs; in a limited series with HW range of 0.94-1.05 mm., CI varied between 84 and 91. Mandibular dentition similar to *niger*, with three or four basal teeth present, but differing statistically in two ways; (1) the four-toothed condition is more common, (2) the second tooth from the basal margin is often bifurcate, a condition rare in *niger*. Forty individuals each representing a different nest series were examined especially for dentition: 16 had three whole basal teeth, 16 had four whole basal teeth, and 8 had a bifurcate second tooth in a set of three. This variation is not allometric, since minimas may have four basal teeth, and it does not appear to have a rigid genetic control, since two adjacent conditions can occur in the same nest series and even on different mandibles of the same individual. The petiole is less variable in outline than in other species of the complex; in all series examined the dorsal margin was shallowly and angularly impressed.

Scape pilosity as described in the diagnosis with the following three exceptions: a series from Dalmatia (H. Kutter leg.; Oxford University Museum) has a preponderance of suberect-erect hairs along the plane of the seta count; two series from Lebanon (Kammouha Plain and Wadi Jahhnam; K. Christiansen leg.; MCZ) lack standing hairs altogether.

Queen. Several interesting character trends have been noted which are, however, of less than diagnostic value. The scutum in profile tends to be more flattened than in other members of the subgenus. The posterior 5/6 of the scutum may be perfectly flat, whereas in *niger* the anterior third or more is usually involved in the anterior declivity. The posterior scutal border (transscutal suture) was found to be markedly sinuate in five out of six specimens examined; in *niger* and other *Lasius s. s.* this border is rarely more than feebly sinuate and often perfectly straight. The punctures of the scutum tend to be deeper and more distinctive in *emarginatus* than in *niger* and *alienus.*

Male. Paramere length 0.24-0.27 mm. in all series examined, apparently varying allometrically with respect to head width to about the same degree as in *niger.* In the total of eight specimens (5 localities) examined for genitalic characters, the setiferous lobes of the subgenital plate showed the same amount and kind of variation as in *niger* (*q.v.*). Two males from the same nest series (Lausanne, Switzerland; M. Bibikoff leg. and Coll.) encompassed the total possible variation, one with a single lobe and the other with two lateral lobes. Seven of the specimens showed the diagnostic outline previously described; one from Milan (USNM) was subquadrate and indistinguishable from *sitkaensis* except in size.

GEOGRAPHIC VARIATION. The alitrunk and petiole color of the worker occasionally deviates from the yellowish red typical of *emarginatus* by deepening to light or medium brownish red, so that the entire body becomes nearly as concolorous as in *niger* and *alienus.* This character may predominate in the Balkans (exclusive of the Trieste area) since all four series I have seen from there possess it: Sofiya, Bulgaria (MCZ); Dalmatia (H. Kutter leg. and Coll.); S. Andrea Is., Dalmatia (Cori leg.; MCZ); Mali Daiti, Albania (MCZ). An intermediate condition, in which the alitrunk and petiole show a lesser degree of infuscation, occurs commonly in eastern Italy and northwestern Yugoslavia (see also under section on distribution): Momiamo, Istria; Cherso; Opcina and Lippizza, near Trieste; San Croce, Venezia Tridentina (all series in MCZ). The typical *emarginatus* coloration has been observed in series from the same localities in two cases, Cherso and Lippizza. It is also noteworthy that material from localities to the south and east of the Balkans (Lebanon, northwestern Iran, Krimea) possess the typical coloration.

There are vague indications of geographic variation in two other characters besides color. The single Krimean series contained the largest workers studied. Two series from Lebanon were the only ones in which standing hairs were completely lacking; suberect and erect hairs attained a maximum relative abundance in the single series from Iran.

DISTRIBUTION. This species appears to be limited to southern Europe and southwestern Asia. Balkan records other than those from northwestern Yugoslavia have already been fully stated in the preceding section. Below are given additional records which have been verified during the course of this revision.

FRANCE: Domfront (E. Lebis leg.; MCZ). SWITZERLAND: Lausanne (M. Bibikoff leg. and Coll.); Yvorne (W. M. Wheeler leg.; MCZ); Monte Generoso (Wheeler leg.; MCZ). AUSTRIA: no further data (G. Mayr leg.; MCZ). CZECHOSLOVAKIA: Kroměríz (O. Fiala leg.; MCZ). ITALY: Cremona, Lombardia (MCZ); Milan (USNM); Parma, Emilia (MCZ); Monte Faito, Sorrento, Campania (MCZ); Venice (Wheeler leg.; MCZ); Lucinico, Venezia Euganea (MCZ); Montello, Venezia Euganea (Ravasini leg.; MCZ); San Croce, Venezia Tridentina (B. Finzi leg.; MCZ); Duino, Divaccia, Lippizza, Opcina, and San Daniele, all near Trieste (Finzi leg.; MCZ); Monte Capanne, Elba, 600 meters (Moczarski-Scheerpeltz leg.; MCZ); Sicily, no further data (Kutter Coll.). YUGOSLAVIA (northwestern): Abbazia, Istria (Kutter leg. and Coll.); Momiamo, Istria (MCZ); Monte Taiano, Istria (B. Finzi leg.; MCZ); Cherso (Ravasini leg.; MCZ). LEBANON: mountain above Kammouha Plain, 1900 meters; Wadi Jahhnam, N. W. Tripoli Prov., 700-1100 meters; Berouk Cedars (all three collections K. Christiansen leg.; MCZ). IRAN: northwestern Iran (Buxton leg.; Oxford University Museum). U. S. S. R.: "Utshan-su" (not located), Krimea (W. Karawajew leg.; MCZ).

Peripheral literature records, which must be taken with great reservation, include Oporto, Portugal (Stitz, 1916; Cephalonia, Ionian Islands (Emery, 1901); and Transcaucasia (Karawajew, 1926). So far as I know no one has claimed to have found this species in North Africa. Wheeler (1927) records "*nigro-emarginatus*" from Teneriffe, Canary Islands, but I have found no material so labelled in his collection.

Goetsch (1937), who has studied the biology of *emarginatus* in detail and seems to have great familiarity with it in the field, states that it is abundant in southern Italy, exceeding *niger* there, but diminishes rapidly toward the north. It is still common in the Italian Alps and Switzerland, ranging up to an elevation of 600 meters. It is very rare and sporadic in southern Germany, being limited to a few warm, dry areas such as the Würzburg Basin, part of upper Silesia, and sections of the Rhine and Neckar valleys.

ECOLOGY. This species nests mostly under rocks in open, dry situations. In Germany Gösswald (1932) found it in orchards, along forest borders, and in wasteland, nesting almost exclusively under rocks and in the crevices of rock walls, and avoiding woodland and moist situations in general. Nowotny (1931) found it uncommon in southwestern Poland, inhabiting dry areas under rocks and in walls. It was found in the same general type of habitat by Scherdlin (1909) in Alsace, by Donisthorpe (1928) in Italy, by Zimmermann (1934) in Yugoslavia, and by Goetsch (1937) in Italy, Switzerland, and Germany. Zimmermann found one colony in the wood of a pine stump on Campo Marzio in the Quarnerian Islands. Gösswald and Goetsch both report that the species occasionally enters houses.

Ecological data accompanying the Lebanon series previously mentioned are of interest because of the peripheral origin of these series (see under distribution). Dr. Christiansen collected the Wadi Jahhnam workers in a valley bottom well shaded by mixed conifers and maples. The ants were foraging above ground along a stream bank. The Kammouha Plain workers were taken well up on a mountainside (1900 meters) under rocks in spruce woods.

Food habits, pastoral activities, and colony founding in this species have been treated briefly by Goetsch (1937). They do not appear to differ fundamentally from those already described for *L. niger* and are not worth bringing into the discussion here.

SYNONYMY. Although I have not seen types of Forel's two "intermediate" varieties *nigro-emarginata* and *brunneo-emarginatus,* the original description indicates that they are no more than insignificant color variants of *emarginatus. Nigro-emarginatus* was characterized by nothing more than a darker alitrunk color (see under geographic variation) and *brunneo-emarginatus* by a lighter alitrunk color and sparser pilosity. Both appear to be well within the normal range of variation for the species.

LASIUS PRODUCTUS Wilson, new species
(Subg. *Lasius*)

DIAGNOSIS. A Japanese species closely related to *L. emarginatus,* but differing in all three castes by the possession of extraordinarily long appendages.

Worker. Within the HW range 0.86-1.12 mm., the SI is between 112 and 124 (see Fig. 5), and the ML exceeds the EW by about 1.3 ×.

Queen. ML in three queens examined ranging 0.32-0.34 mm., exceeding all other members of the genus.

Male. SI of the one specimen measured was 105, greatly exceeding all other members of the genus.

HOLOTYPE. A worker from Mt. Imano (Imanoyama), Shikoku (H. Okamoto leg. and Coll.). PW 0.72 mm., HW 1.04 mm., HL 1.17 mm., SL 1.23 mm., SI 119, ML 0.30 mm., EW 0.22 mm. Paranidotypes in the Yasumatsu Coll., MCZ, USNM, and Holgersen Coll.

FURTHER DESCRIPTION. *Worker.* Size averaging larger than in other members of the subgenus; PW 0.59-0.73 mm., mean 0.686 mm., based on 15 workers from 6 nest series. Anterior border of median clypeal lobe broadly rounded as in other *niger* complex members. Dentition very constant, with three perfectly formed basal teeth in every specimen examined. Propodeum elevated relative to thorax as in *emarginatus*. Scapes densely covered with predominantly decumbent hairs; standing hairs very scarce or absent. Tibiae with sparser hairs which are mostly appressed. Color varying from concolorous medium brown as in *niger* (e.g. paratypes from Hikosan VIII-6-1940 and Sobosan IX-8-1933) to bicolorous with contrasting reddish brown alitrunk and dark brown gaster and head (e.g. paratypes from Hikosan XI-21-1939). The holotype nest series falls about intermediate between these two extremes; the holotype can best be described as having a medium reddish brown alitrunk barely contrasting with the gaster. None of the material examined reaches the extreme bicolorous condition of the typical European *emarginatus;* moreover, in *productus* the head is usually noticeably lighter than the gaster.

Queen. Characterized by its higher SI and tendency toward larger size. Following are measurements for three queens identified in the course of the present study. Japan, no further data (H. Sauter leg.; MCZ), HW 1.88 mm., SL 1.58 mm., SI 84, ML 0.32 mm.; Hikosan, Kyushu, IX-18-1939 (K. Yasumatsu leg. and Coll.), HW 1.79 mm., SL 1.55 mm., SI 87, ML 0.32 mm.; Hirooka, Shikoku VIII-29-1935 (H. Okamoto leg. and Coll.), HW 1.82 mm., SL 1.52 mm., SI 84, ML 0.34 mm.

Male. In the single specimen examined (Sobosan, Kyushu, IX-10-1933; Yasumatsu leg. and Coll.), HW 0.98 mm., SL 1.03 mm., SI 105. Subgenital plate very similar to that typifying *emarginatus*. Scapes densely covered with rather short, predominantly subdecumbent hairs. Tibiae with sparse, appressed to decumbent hairs.

DISTRIBUTION. Following are all of the records of the new species accumulated during the present study. KYUSHU: Hikosan (3 series; Yasumatsu, Esaki, and Nomura leg.; Yasumatsu Coll. and MCZ); Inugatake (Hori, Kawahara, and Yasumatsu leg.; Yasumatsu Coll. and MCZ); Sobosan (Yasumatsu leg. and Coll.); Sefuriyama (Yasumatsu leg. and Coll.). SHIKOKU: Imanoyama (holotype nest series); Hirooka, winged queen (Okamoto leg. and Coll.). HONSHU: Arima, near Kobe (M. Azuma leg.; USNM). TSUSHIMA: Isuhara-Sasutôge (Shirôzu leg.; Yasumatsu Coll.).

LASIUS NEONIGER Emery
(Subg. *Lasius*)

Lasius niger var. *neoniger* Emery, 1893, Zool. Jahrb. Syst, **7**: 639; worker; original description. Type locality: Virginia; by present restriction.
Lasius neoniger, Wheeler, 1910, Psyche, **17**: 83.
Lasius neoniger, E. Gregg, 1945, Ann. Ent. Soc. Amer., **38**: 534.
Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 420, part.

DIAGNOSIS. *Worker and queen.* Possessing the first two of the following characters in common with the other two members of the "*neoniger* complex" (*crypticus* Wilson and *sitiens* Wilson) and differing from these two species by the possession of the third.

(1) At least 20 per cent and often more than 90 per cent, of the nest series with the median of three basal teeth reduced in size relative to the two flanking teeth (see Pl. 1, fig. 3); in individuals where this tooth is absent, the space between the two remaining teeth is typically irregular in size and shape and usually larger in area than the basal-most tooth.

(2) The anterior border of the median clypeal lobe, when viewed in perfect full face (attaining maximum head length) and with the mandibles open, is obtusely angulate, the lateral faces straight and often meeting centrally to form a distinct angle (see Pl. 1, fig. 3); opposed to the broadly convex or parabolic condition of the "*niger* complex."

(3) Scapes and fore tibiae with abundant hairs, many of which are standing. The density declines allometrically, and nanitic workers (with PW about 0.40 mm.) may have seta counts of 0.

Male. Very similar to small individuals of *L. niger* except that the anterior border of the median clypeal lobe tends to be angulate as in the worker and queen. In the male this character is highly variable, however, and not all isolated individuals can be determined to species with certainty.

LECTOTYPE. By present selection, a worker in the Emery Collection labelled "Va.". PW 0.49 mm., HW 0.75 mm., SL 0.73 mm., SI 97, seta count 16. Typical for the species in dentition, clypeus, pilosity, and color.

FURTHER DESCRIPTION. *Worker.* PW 0.39 mm. (incipient colony) to 0.64 mm.; the range and dispersion are apparently about the same as for *alienus* (*q. v.*). SI of series of average-sized to large workers falling in the *niger-alienus* regression zone, although two nanitics measured (Sudbury, Mass. incipient colony; Wilson leg.; MCZ) fell lower, just above the extrapolated *brunneus* zone — SL/HW ratios were 0.59/0.57 mm. and 0.59/0.58 mm. respectively. A similar dip in the regression zone has been observed in the sibling species *L. crypticus,* while the third member of the *neoniger* complex, *L. sitiens*, falls along the extrapolated *brunneus* zone. This indicates that the *neoniger* complex differs generally from the *niger* complex by having steeper regression zones. In body form, head shape, petiolar variation, etc., *neoniger* closely resembles *niger* and *alienus.* Appendage pilosity sparser and averaging shorter than in *niger*, with more hairs inclining to decumbent-subdecumbent, which condition occurs in *niger* in the Asiatic population only. Maximum color variation has been encountered within collections from the western U. S.: series from the White Sands National Monument, New Mexico, range to pale yellowish brown, with the head slightly darker than the remainder of the body; a series from Bishop, California, is a shade of dark brown about average for *niger* and *alienus.* The usual *neoniger* coloration is a light brown with feebly contrasting darker head.

Queen. Size range and dispersion apparently about the same as for *L. alienus.* The dentition and clypeal characters of the worker are repeated in this caste with exaggerated effect. The clypeus is typically very angular, contrasting with the evenly convex condition of the *niger* complex and the flat-to-emarginate condition of *sitkaensis.* A peculiarity of the dentition in this caste is the frequent occurrence of an offset basal tooth similar to that characterizing *sitkaensis;* but when this occurs, it is often present on one mandible only, it is usually larger and more acute than in *sitkaensis*, and it is rarely if ever accompanied by secondary teeth on the basal border. The wings are more opaque than in the *niger* complex but lack the pattern of basal infuscation characterizing *sitkaensis* and *brunneus.*

Male. HW 0.74-0.86 mm., dispersion apparently about the same as for the North American populations of *niger* and *alienus.* Genitalia size and configuration, including the posterior lobing of the subgenital plate, apparently the same as for these two species.

GEOGRAPHIC VARIATION. Series from the western United States, from Montana south to New Mexico and west to California, show the greatest total variability in size, color, and pilosity, but there is no definable unilateral trend in any single character. Four series taken in pure sand in the White Sands National Monument, New Mexico, are exceptionally hairy and light in color, both of which characters may represent adaptation

Fig. 9. An outline of the known distribution of *L. neoniger*.

on the part of the local population to the extreme environment at this locality.

DISTRIBUTION. (See also Fig. 9). *L. neoniger* is abundant in eastern North America and as far west as North Dakota and Iowa. West of the Great Plains it apparently diminishes rapidly; it is rather uncommon in the southern Rockies and is thus far completely unknown from the Pacific Northwest.

In the summer of 1952 I found it to be one of the dominant species of ants in a number of localities visited in southern Quebec and Ontario, including Montreal, Verdun, Lake Constance, Deux Rivieres, North Bay, Sturgeon Falls, and Blind River. Other southeastern Canadian records verified during the present study include Toronto (R. J. Crew leg.; MCZ) and Cloyne, Ont. (A. B. Klugh leg.; MCZ). There is no way of determining the northern limits of the species with available data.

Neoniger is one of the dominant ants in open habitats everywhere from New England to North Carolina and Tennessee. I found it extremely abundant in the vicinity of Washington, D. C., and Great Falls, Va., and at lower elevations in western North Carolina and eastern and central Tennessee. It maintains this abundance in the region of the Great Smoky and Black Mountains up to an elevation of about 5100 feet. At the latter elevation, on the southern slope of Mt. Mitchell, I found the species to drop off sharply, and so far as I know neither A. C. Cole, A. Van Pelt, nor I have ever collected it higher than this in the course of many field trips in the area.

The species has been taken in several localities in South Carolina (first four series in USNM): Batesburg, Lexington Co. (E. S. Titus leg.); Saluda Co.; Marion, Marion Co. (C. G. Ainslee leg.); Clemson College, Pickins Co. (M. R. Smith leg); Myrtle Beach State Park, Horry Co. (W. S. Creighton leg. and Coll.). It is rare in the Gulf States, being known only from the following several localities: Seeley's Pond, Seminole Co., Ga. (P. B. Kannowski leg.; UMMZ); Jackson Co., Fla. (Kannowski leg.; UMMZ); Tuscaloosa, Ala. (E. O. Wilson leg.; MCZ); Eufaula, Barbour Co., Ala. (Wilson leg.; MCZ).

Neoniger is abundant throughout North Dakota, as shown by the massive collections made by G. C. Wheeler and his students. I have seen material from South Dakota (Capa, Jones Co., MCZ; Brookings, H. C. Severin leg., MCZ), Nebraska (Grand Island,

R. P. Uhlmann leg., G. C. Wheeler Coll.; McCook, Redwillow Co., USNM; North Platte, Cole leg. and Coll.), and from various localities over Kansas (University of Kansas Coll., USNM, MCZ). I have seen a single series from Ware, Dallam Co., Texas (USNM), the only record of the genus from that state known to me.

Following are records from west of North Dakota and Texas which have been accumulated during the present study. MONTANA: Harlem, Blaine Co. (E. O. Wilson leg.; MCZ); Great Falls Air Base (Wilson leg.; MCZ). IDAHO: Hagerman, Gooding Co. (A. C. Cole leg. and Coll.); Twin Falls (Cole leg. and Coll.); Castleford, Twin Falls Co. (Cole leg. and Coll.). WYOMING: Guernsey, Platte Co. (USNM). COLORADO: Rist Canyon, Fort Collins (USNM); Denver (W. M. Wheeler leg.; MCZ); Salida, Chaffee Co. (Wheeler leg.; MCZ); Silverton, San Juan Co. (E. J. Oslar leg.; MCZ). NEW MEXICO: Albuquerque (L. D. Christenson leg., USNM; W. M. Wheeler leg., MCZ); White Sands National Monument, 4 series (Cole leg. and Coll.). CALIFORNIA: Bishop (Wilson leg.; MCZ); Yuba City (L. D. Christenson leg.; MCZ). There is an excellent possibility that the California records represent disjunct introduced populations, since they were both found in heavily populated areas.

There is in the United States National Museum a long uninidal series of *neoniger* labelled "Anchorage, Alas / 1947 / VIII-47 / F. R. DuChanois." I have contacted Lt. DuChanois and he assures me (*in litt.*) that this extraordinary record is to the best of his knowledge valid. He believes that the collection was made in the vicinity of the 18 milepost on the Anchorage-Fairbanks highway. "Most of the Formicidae were taken in pine-birch-(and occasionally hemlock) forested areas on the open ground . . . I am quite certain that the specimens did not represent transient incursions because of the relative remoteness of the ecological habitats in which they were taken." Nevertheless, the considerable range extension that this record represents for the genus, with the nearest specific record for *L. neoniger* in southern Idaho, makes it desirable to withold judgment until additional material can be secured.

ECOLOGY. This species nests almost exclusively in open areas, either under stones or in open soil in craters. In the eastern United States it is frequently the dominant ant in grassy road strips, lawns, cultivated fields (cf. Talbot, 1953), and other disturbed situations. By virtue of this ruderal adaptation it has become one of the most abundant and conspicuous insects within its range. The only natural habitats in which I have found it dominant are prairie (North Dakota, Montana) and old beach dunes (New England coast, Great Lakes). It never penetrates deep forests and is scarce in open woods and well shaded forest borders.

One of the most interesting features of its ecological distribution is its clearcut microgeographic replacement by the woodland species *L. alienus.* The two species overlap to a limited extent in open, sunny woodland, where both may be found nesting under stones. But the bulk of the *neoniger* population occurs in completely exposed situations, in craters and under stones, while most of the *alienus* are in rotting stumps and logs in well shaded woodland. This replacement pattern can be developed into an intricate mosaic where the habitats are suitable. Such a situation is found at Ipswich Beach, Massachusetts, for example, where the two species occur together in a small stretch of littoral woodland covering about fifty acres. The woods at this locality consist principally of small trees of *Betula populifolia* (grey birch), *Prunus maritima* (beach plum), *Acer rubrum* (red maple), *Pinus rigida* (pitch pine), and several species of oak. They are dense in low swampy areas where they provide leaf litter and humus of varying thickness to the loose, sandy soil. They are broken at intervals however, by foot paths, animal trails, and sand ''blowouts''. The latter are shallow, barren depressions in the sand in which only scattered grass and *Hudsonia* shrubs grow. *L. neoniger* is limited to these open areas, its craters often occurring in dense concentrations where the sand is firmly packed and moist several inches below the surface. *L. alienus,* on the other hand, is entirely limited to rotting stumps, logs, and branches on the shaded forest floor. Under natural conditions there is probably always an ample supply of such nesting sites, since *Betula populifolia,* the dominant tree, is very short-lived, and dead trees must always be in abundance. The two species are thus sharply segregated ecologically, with the *neoniger* population consisting of a series of enclaves within a more or less continuous woodland *alienus* population. No instances of overlap were found; the closest approach was a colony of *alienus* in a rotting log near the margin of a blowout and about seven feet from a cluster of *neoniger* craters.

Like other species of *Lasius*, *neoniger* is polyphagous, accepting both insect food and nectar. At Schroon Lake, N. Y. and Lake Constance, Ontario, I watched workers of this species foraging above ground in the early part of the night. The "trophophoric field" of the many nests observed did not seem to exceed two or three yards in radius, and the workers appeared to be engaged solely in gathering dead and crippled insects. A great variety of insects were accepted, including flies, leafhoppers, beetles, and spiders of various sizes. Using captive colonies maintained during a period of over a year, I have since learned that insects are readily accepted as food and are evidently necessary for successful colony growth.

The pastoral habits of this species have been dealt with in detail by S. A. Forbes' classic account (1894). He and later authors, including W. M. Wheeler, have referred to the species studied as "*americanus*" (treated herein as a synonym of *alienus*), but there can be little doubt, judging from the descriptions of the ecology, nesting habits, etc., as well as from a drawing later published by Forbes, that it was really *neoniger*. The mutualistic relationship between the *Lasius* and the cornroot aphid (*Aphis maidiradicus*) as explored by Forbes is very similar to that later demonstrated by Eidmann (1926) between the European *L. niger* and an epigaeic species of aphid. The ants gather the eggs of the fall sexual brood of the aphid, store them in the nests over the winter, and in the spring excavate special galleries by means of which they are able to place the newly hatched nymphs directly on the corn roots. When strange aphids are freshly presented to the ants above ground they are promptly carried into the nest and placed on the roots also.

Talbot (1946) has studied diurnation in this species. In ordinary summer weather the workers are mainly nocturnal. Activity begins to rise in late afternoon, continues through the night, and declines through the following morning. The species prefers cool temperatures (50°-60° F.) and high humidity.

Forbes (1908) and Tanquary (1913) have studied the life history of this species in some detail. Nuptial flights are recorded by them for the period September 5-October 18. Mr. B. D. Valentine (pers. commun.) has observed nuptial flights of this species on Long Island, New York, during the first week of September over a period of several years. It has been my observation that flights occur mainly in September in the Boston area also. The earliest record for a flight is one which I observed at Bishop, California, on July 30, 1952. In so far as I know the flights always take place during the second half of the afternoon; the one at Bishop continued to dusk. In the collections available to me, I have found winged forms associated in the nest with workers from July 25 (Salida, Colo.) to October 13 (Denver, Colo.). Forbes and Tanquary both showed that colony founding in this species resembles that later described for *niger* and *flavus* by Eidmann (1931). The fecundated queens overwinter without brood and start laying eggs in the following spring.

LASIUS CRYPTICUS Wilson, new species

(Subg. *Lasius*)

DIAGNOSIS. A western North American species very similar to *L. neoniger,* differing principally in the scarcity of hairs on the scapes and fore tibiae, and by the darker body coloration of the worker and queen. Linked to the "*neoniger* complex" by the possession of clypeal and dentition characters already detailed in the description of *neoniger*. Superficially resembles *alienus* and has been consistently determined as this species ("*americanus*") by past authors.

(1) In all three castes standing hairs are invariably absent on the scapes and fore tibiae along the plane of count (seta count, *q. v.*), while appressed decumbent hairs are rare or absent. These surfaces are covered only by a short, predominantly appressed pubescence.

(2) The worker and queen are almost invariably dark brown, rarely medium brown, opposed to the typically light brown coloration of *neoniger*. The males of the two species show broadly overlapping dark brown coloration.

(3) The worker has a proportionately shorter scape length than in *neoniger;* a small number of series of medium-sized to large workers, when measured, fell between the *alienus-niger* and *brunneus* SI-HW regression zones, while several nanitic series fell along the extrapolated *brunneus* zone. However, *crypticus*

and *neoniger* are too close to give this character diagnostic value by itself.

HOLOTYPE. A worker in the MCZ, selected from a large nest series collected four miles north of Gardar, Pembina Co., N. Dak., Aug. 31, 1949, with associated winged queens and males (E. L. Krause leg., acc. no. 138). PW 0.52 mm., HW 0.79 mm., SL 0.70 mm., SI 90, EL 0.19 mm., seta count 0. Fits the *neoniger* complex

Fig. 10. An outline of the known distributions of *L. crypticus* and *L. sitiens.*

in clypeus and dentition characters and is distinguished specifically by pilosity and color. Paranidotypes are in the MCZ, USNM, UMMZ, G. C. Wheeler Coll., Creighton Coll., and Cole Coll.

DISTRIBUTION. *Crypticus* has its center of abundance in the Great Plains of the western U. S. It apparently stops abruptly at the edge of the eastern deciduous forest, having never been collected east of the eastern tier of counties of North Dakota. It is relatively common in the Rocky Mountains and Great Basin, and reaches as far west as California and Oregon. In the following list are included all of the records accumulated during the present study. (See also Fig. 10.)

NORTH DAKOTA (all series in G. C. Wheeler Coll., except where otherwise noted; most with nest duplicates in MCZ): Pembina Co. (E. L. Krause leg., accession nos. 175, 178); Walsh Co. (W. E. LaBerge leg., acc. nos. 14, 15, 57, 91, 93, 94, 97, 99, 110, 117, 118, 119, 126, 132, 134, 233, 244, 251); Grand Forks Co. (J. N. Wheeler leg., acc. No. 9; L. Monda leg., acc. no. 901); Cass Co. (C. Schonberger leg., acc. nos. 5, 21, 34, 71, 141); Richland Co. (H. H. Osborn leg., acc. nos. 2, 23, 105, 133, 158, 159, 172, 183, 227); Ramsey Co. (UMMZ; P. B. Kannowski leg., acc. nos. 34, 51, 154, 176, 186, 326); McClean Co. (R. P. Uhlmann leg., acc. nos. 211, 216, 226, 256); Divide Co. (J. Davis leg., acc. nos. 8, 11, 12, 25, 50, 51, 57, 58, 66, 67, 76, 79, 82, 108, 110, 148, 149, 187, 188, 189, 190, 191, 192, 193, 194, 196, 198, 200, 209); Billings Co. (J. E. Goldsberry leg., acc. nos. 100, 150, 157); Golden Valley Co. (J. E. Goldsberry leg., acc. nos. 103, 105, 110); Stark Co. (R. P. Uhlmann leg., acc. no. 90); Slope Co. (Black Butte; E. and G. Wheeler leg.); Hettinger Co. (R. P. Uhlmann leg., acc. nos. 3, 6, 9, 23, 25). (While relatively common in several of the easternmost counties of North Dakota, *crypticus* was not present in a large collection of the genus made by Mr. Kenneth Kraft in Itasca State Park, Minnesota, nor has it been taken anywhere else in that state.) SOUTH DAKOTA: Capa, Jones Co. (MCZ); Hill City (T. Ulke leg.; MCZ). MONTANA: Culbertson, Roosevelt Co. (E. O. Wilson leg.; MCZ); Great Falls (Wilson leg.; MCZ). ALBERTA: Lethbridge (G. G. Hewitt leg.; MCZ). IDAHO: Hagerman, Gooding Co. (A. C. Cole leg. and Coll., MCZ); Twin Falls (2 series, Cole leg. and Coll., MCZ); Green Canyon Hot Springs, Madison Co. (B. Malkin leg. and Coll., MCZ); Donnelly and Cascade, Valley Co. (Wilson leg.; MCZ). WYOMING: Madison Junction, Yellowstone Nat. Pk. (Wilson leg.; MCZ); Dubois, Fremont Co. (W. S. Creighton leg. and Coll.). COLORADO: Boulder (W. M. Wheeler leg. and S. A. Rohwer leg., both MCZ; Creighton leg. and Coll.); South Boulder Canyon (T. D. A. Cockerell leg.; MCZ); Cheyenne Canyon, Colorado Springs (MCZ); Florissant, Teller Co. (Wheeler leg.; MCZ); Buena Vista, Chaffee Co. (Wheeler leg.; MCZ) Creede, Mineral Co. (S. J. Hunter leg.; MCZ). NEW MEXICO: Capulin Mt. Nat. Mon., Union Co., 7100 feet (Cole leg. and Coll., MCZ); 10 miles west of Cimarron, Colfax Co., 7100 feet (Cole leg. and Coll., MCZ); 16 miles east of Raton, Colfax Co., 6650 feet (Cole leg. and Coll., MCZ); 2 miles south of Raton Pass, 7700 feet (3 series, Cole leg. and Coll., MCZ); 11 miles north of Eagle Nest, in Taos Co., 9000 feet (Cole leg. and Coll. MCZ); 12 miles east of Taos, 7250 feet (2 series, Cole leg. and Coll., MCZ). UTAH: Henry Mts., Garfield Co. (Creighton leg. and Coll., MCZ); Long Valley Junction, Kane Co. (Wilson leg.; MCZ). CALIFORNIA: Hurkey Creek Camp Grounds, San Jacinto Mts. (Creighton leg. and Coll., MCZ). OREGON: Durkee, Baker Co. (B. Malkin leg. and Coll., MCZ).

ECOLOGY. The following generalizations are based on a few of my own observations along with field notes supplied me by G. C. Wheeler, A. C. Cole, and Borys Malkin. *Crypticus* is most abundant in prairies and tends to replace *neoniger* in the most dry, exposed situations. In eastern Montana and southern Idaho it was found thriving in a short-grass prairie-semidesert transition. At Cascade, Idaho, and in several localities in New Mexico, it was taken in open pine forest. At Green Canyon Hot Springs, Idaho, it was found in dry willow-poplar woods. In the great majority of cases it has been found nesting under stones, but occasionally (e.g. Donnelly and Cascade, Idaho) it constructs *neoniger*-like craters in open soil.

No nuptial flights of this species have been recorded. Winged reproductives have been taken with workers from July 9 (Great Falls, Mont.) to August 31 (holotype nest series, Pembina Co., N. Dak.). The majority of such records fall in the last half of July and first half of August. This would seem to be strong prima-facie evidence that the reproductive period of *crypticus* precedes that of *neoniger*.

LASIUS SITIENS Wilson, new species

(Subg. *Lasius*)

DIAGNOSIS. A small, light-colored species occurring in the southwestern United States and northern Mexico.

Worker. (1) The outstanding diagnostic character is the small eye size: maximum eye length (EL) only 0.21-0.25 × the HW, whereas it always exceeds 0.25 × the HW in *neoniger* and *crypticus* and members of the *niger* complex. The maximum ommatidium number in a line along the long axis of the eye is typically 11 in *sitiens,* and occasionally 10 or 12; in related species it is typically 14 or 15 and occasionally 13 or 16.

(2) Averaging smaller than other members of the subgenus; PW rarely exceeding 0.56 mm. and usually less than 0.54 mm.

(3) Scapes and tibiae lacking standing hairs.

(4) Color typically medium yellowish brown, rarely dark yellowish brown.

Queen. Very similar to the queen of *crypticus,* differing only in the following two characters.

(1) Averaging and ranging smaller; HW range in all available series 0.63-0.78 mm.

(2) Body medium to dark brown, with pale yellowish brown legs.

Male. In this caste the anterior border of the median lobe of the clypeus is broadly rounded, in contradistinction to the angular condition of the worker and queen of the same species, and males of *neoniger* and *crypticus.* Individuals are therefore not surely separable from small, faded *alienus* males. The following two characters represent distinctive trends but are not absolutely diagnostic.

(1) Averaging and ranging smaller than other members of the subgenus; HW range in all available series 0.63-0.78 mm.

(2) Body medium to dark brown, with pale yellowish brown legs.

HOLOTYPE. A worker in the MCZ, selected from a nest series collected 20 miles north of Flagstaff, Arizona, on U. S. Route 89, July 25, 1952, with associated winged queens and males (E. O. Wilson leg.). PW 0.50 mm., HW 0.71 mm., SL 0.68 mm., SI 95, EL 0.17 mm., 11 ommatidia counted along the long axis of the eye. Paranidotypes in MCZ, USNM, and Creighton Coll.

FURTHER DESCRIPTION. *Worker.* PW maximum range 0.40-0.56 mm. In a sample of 53 from as many nest series, mean with standard error 0.472 ± 0.006 mm., standard deviation 0.042 mm. Appendages noticeably shorter than in related species. Scape index low, falling along the extrapolated *brunneus* SI-HW regression zone, but overlapping the lower extremity of the *crypticus* zone. The funiculus is also shortened, to the extent that flagellar segments I and II are as broad as long or slightly (never more than 1.3 ×) broader than long, and segment III is as broad as long to slightly longer than broad; most of the range of this variation may be seen in single nest series. Maxillary palp segments V and VI subequal, quite short with respect to total body size, so that their length varies between 0.5 × and 0.8 × the maximum fore-tibia width. The head shape is slightly divergent from that of other species in that the largest workers show a "mature" allometric broadening of the head just behind the eyes; i.e. the allometric variation in head shape seen in larger species is expressed on a more diminutive scale in this species. Scapes and fore tibiae ordinarily devoid of hairs of any sort, although several decumbent to subdecumbent hairs were observed on the scapes in a single series from Sapello Canyon, New Mexico.

GEOGRAPHIC VARIATION. No trends were detected within the rather limited range of this species.

DISTRIBUTION. Below are listed all of the records of the new species accumulated during the present study. (see also Fig. 10).

COLORADO: Salida, Chaffee Co. (W. M. Wheeler leg.; MCZ); Canon City, Fremont Co. (Schmitt leg.; MCZ); Mesa Verde Nat. Pk. (A. C. Cole leg. and Coll., MCZ; B. Malkin leg. and Coll., MCZ); Trinidad, 6500 feet, 2 series (Cole leg. and Coll., MCZ). NEW MEXICO: Ute Park, Colfax Co., 7400 feet (2 series, Cole leg. and Coll., MCZ); Cimarron Canyon, 6 miles north of Ute Park, 7750 feet (Cole leg. and Coll., MCZ); 15 miles east of Taos, 8000 feet (Cole leg. and Coll., MCZ); 4 miles south of Los Alamos, 6400 feet (Cole leg. and Coll., MCZ); 5 miles south of Beulah, San Miguel Co., 7200 feet (Cole leg. and Coll., MCZ); Sapello Canyon, Beulah area, 8000 feet (Cole leg. and Coll., MCZ); Dailey Canyon, Beulah area (Cole leg. and Coll., MCZ); Bandelier Nat. Mon., 4 series at 6350 feet, 1 at 6050 feet

(Cole leg. and Coll., MCZ); Otowi Entrance, Bandelier Nat. Mon., 6100 feet (5 series, Cole leg and Coll., MCZ); Pecos (T. D. A. Cockerell leg.; MCZ); Albuquerque (MCZ); Mogollon Mt., Catron Co., 8600 feet (Cole leg. and Coll., MCZ). ARIZONA: Indian Garden and Coconino Forest, Grand Canyon (W. M. Wheeler leg.; MCZ); 20 miles north of Flagstaff (holotype nest series; also 1 series Cole leg. and Coll., MCZ); Flagstaff, south slope of San Francisco Peaks, 7000 feet (Wilson leg.; MCZ); Prescott (Wheeler leg.; MCZ); Oracle, Pinal Co., 4500 and 5000 feet (2 series, Wheeler leg.; MCZ); Stratton, Santa Catalina Mts., 6000-7000 feet (Wheeler leg.; MCZ); Miller Canyon, Huachuca Mts., 4800 and 5600 feet (2 series, Wheeler leg.; MCZ); Ramsey Canyon, Huachuca Mts. (W. S. Creighton leg. and Coll.); Campground, Chiricahua Mts., 5400 feet (Creighton leg. and Coll.); Campbell Blue Creek, Apache Nat. Forest (Creighton leg. and Coll.). DURANGO: 32 miles west of El Salto, 8700 feet (2 series, Creighton leg. and Coll.).

ECOLOGY. This species is limited to the lower altitudinal forest belts in the mountains of the Southwest, from juniper scrub at 7000 feet or less to mixed pine-spruce at 8000 feet. Judging from ecological notes accumulated by W. M. Wheeler, Cole, and myself, it nests almost exclusively under stones in dry, open situations. The type locality is situated in an area of open juniper scrub and scattered bunch-grass. *Sitiens* is co-dominant at this spot with several species of *Myrmecocystus, Pogonomyrmex*, and *Conomyrma*. At the base of the San Francisco Peaks, near Flagstaff, I found *sitiens* again abundant, nesting under rocks in open pine forest. In New Mexico Cole has taken *sitiens* primarily in pine forest and clearings bounded by pine forest. The ecological extremes in which he collected this species are as follows: near Los Alamos, a nest in an open, grassy area with scattered pine and juniper at 6400 feet; near Taos, a nest in moist pine-spruce woods at 8000 feet.

The light coloration, small eyes, and shortened appendages of *sitiens* constitute a remarkable morphological convergence to the species of the subgenus *Cautolasius,* and specifically to the primitive species *L.* (*C.*) *alienoflavus*. There can be little question that the characters shared by these two species are the mark of a subterranean mode of life. At the type locality I was unable to find any workers foraging above ground either during the day or in the early night; in contrast, wherever the related species *neoniger* occurs its workers can nearly always be found above ground at any time of the day or night.

No nuptial flights of *sitiens* have been recorded. Reproductives have been taken *in nido* on six occasions, from July 2 (Campbell Blue Creek, Apache Nat. For., Ariz.) to July 30 (Bandelier Nat. Mon., N. Mex.). This would seem to indicate an early reproductive period similar to that of *L. crypticus.*

LASIUS ALIENOFLAVUS Bingham
(Subg. *Cautolasius*)

Lasius alieno-flavus Bingham, 1903, The Fauna of British India (Taylor and Francis, London), Hymenoptera, **2**: 341; worker; queen; original description. Type locality: Indian Himalayas, above 8000 feet.

DIAGNOSIS. *Worker.* The three specimens examined are indistinguishable from northern Eurasian *flavus* of comparable size except for their longer maxillary palps and the fact that segment VI is longer than segment V. The right maxillary palp of a specimen in the MCZ measured as follows: segment III 0.15 mm., IV 0.11 mm., V 0.08 mm., VI 0.09 mm. *Flavus* workers of the same approximate size have much shorter segments: segment III probably never exceeds 0.13 mm., IV, 0.08 mm., V, 0.06 mm., or VI, 0.06 mm., and these segments are usually distinctly shorter. In this character *alienoflavus* actually overlaps the lower limits of the subgenus *Lasius: L. sitiens* workers of comparable size have approximately the same segment proportions.

TYPES. I have seen two workers in the AMNH and one in the MCZ labelled "N. Indien, I. XXXVII (Wroughton) / L. alieno-brunneus var. alieno-flavus For." From Bingham's description and comments it seems certain that these are part of the type nest series, but they were probably sent by Forel directly to Wheeler in the AMNH without first having been examined by Bingham. I do not think therefore it would be a valid procedure to select one as lectotype. The MCZ nidotype gives the following measurements: PW 0.51 mm., HW 0.76 mm., SL 0.70 mm., SI 92, EL 0.13 mm., ommatidium number 36 and 39. A second intercalary tooth is lacking in the one exposed (left) mandible. Petiole feebly emarginate. Cephalic pubescence dilute, as described for the eastern North American population of *flavus* (see under geographic variation of that species). Head shape difficult to judge at this size, apparently "intermediate" (eastern North American *flavus-nearcticus*) approaching the *nearcticus* form, probably also within the range of variation of the Eurasian *flavus*. Otherwise identical to *flavus*. PW of AMNH nidotypes 0.44 and 0.48 mm.

Lasius flavus (Fabricius)

(Subg. *Cautolasius*)

Formica flava Fabricius, 1781, Species Insectorum, **1:** 491; worker; original description. Type locality: northern Europe.

Lasius brevicornis Emery, 1893, Zool. Jahrb. Syst., **7:** 639–640; worker, queen, male; original description. Type locality: District of Columbia; selected by Creighton (1950). NEW SYNONYMY.

Lasius flavus myops Forel, 1894, Bull. Soc. Vaud. Sci. Nat., **30:** 12; worker; original description. Type locality: Terni, Oran, Algeria. NEW SYNONYMY.

Lasius flavus var. *myops*, Emery, 1916, Bull. Soc. Ent. Ital., **47:** 167.

Lasius flavus myops var. *flavoides* Forel, 1894, *ibid.*, p. 12; worker; original description. Type locality: Fully, Switzerland. NEW SYNONYMY.

Lasius flavus var. *fuscoides* Ruzsky, 1902, Formicariae Imperii Rossici, Schrift. Naturforsch. Ges. Univ. Kasan, **38:** 281. Type locality: U.S.S.R. NEW SYNONYMY.

Lasius flavus var. *odoratus* Ruzsky, 1902, *ibid.*, pp. 282-283; worker; original description. Type locality: U.S.S.R. NEW SYNONYMY.

Lasius flavus var. *flavo-myops* Forel, 1915, Fauna Insect. Helv. Hym. Formicid. (Mitt. Schweiz. Ent. Ges., vol. 12), p. 52. NEW SYNONYMY (objective synonym of *flavoides* Forel).

Lasius brevicornis microps Wheeler, 1917, Proc. Amer. Acad. Arts Sci., Boston, **52:** 526; worker; original description. Type locality: Camp Curry, Yosemite Village, California, 4000 ft. NEW SYNONYMY.

Lasius flavus microps, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 422.

Formicina flava var. *morbosa* Bondroit, 1918, Ann. Soc. Ent. Fr., **87:** 28–29; worker, queen; original description. Type locality: France. NEW SYNONYMY.

Lasius umbratus var. *apennina* Menozzi, 1924, Atti Soc. Nat. Mat. Modena, **8:** 15; worker; original description. Type locality: Val Gorgo, Modena Apennines, Italy. NEW SYNONYMY.

Lasius flavus var. *apennina*, Menozzi, 1932, Boll. Ist. Ent. Bologna, **5:** 8–9.

Lasius umbratus ibericus Santschi, 1925, Eos, **1:** 349–350; worker; original description. Type locality: Camprodón, Gerona, Spain. NEW SYNONYMY.

Lasius umbratus ibericus var. *sancho* Santschi, 1925, *ibid.*, p. 350; worker; original description. Type locality: Panticosa, Huesca, Spain. NEW SYNONYMY.

Lasius flavus var. *olivacea* Karawajew, 1926, Konowia, **5**: 194; worker; original description. Type locality: Turugai River, Dschewanschir region, Elizabethpol District, U.S.S.R. NEW SYNONYMY.

Lasius helvus Cook, 1953, The Ants of California (Pacific Books, Palo Alto, Calif.), p. 326, fig.; worker; original description. Type locality: Lake Tahoe, Calif. NEW SYNONYMY.

Lasius helveolus Cook, 1953, *ibid.*, p. 327. NEW SYNONYMY (objective synonym of *helvus* Cook).

DIAGNOSIS. *Worker and queen.* In the eastern United States, where *flavus* occurs sympatrically with *L. nearcticus*, it can be separated from this and other *Cautolasius* by a host of characters, but elsewhere these are subject to much geographic variation and tend to break down and lose their diagnostic value. Only one character has been found which will consistently separate all Nearctic and Palaearctic *flavus* populations from *nearcticus* (no. 1 below).

(1) Maxillary palp segment V as long as segment VI or longer.

(2) A much weaker character is found in the petiolar outline. In *flavus* the dorsal margin in frontal view is usually emarginate to flat, while in the majority of *nearcticus* it is convex.

(3) In addition, *flavus* can be separated from the related species *L. fallax* (Wilson) and *L. talpa* (Wilson) by the following character: scapes and outer tibial surfaces lacking standing hairs.

Male. Isolated individuals cannot be separated with certainty from other members of the subgenus.

(1) The subgenital plate tends to be subquadrate, with a protruding posteromedian setiferous area. This character will separate a majority of series from *nearcticus*.

(2) The outer femoral surfaces in *flavus* are ordinarily bare of standing hairs, separating this species from *fallax* and doubtfully from *talpa*.

FURTHER DESCRIPTION. *Worker.* (See also under geographic variation.) Mandibular dentition follows certain recognizable trends specific at least for the subgenus. In large specimens from northern Europe there are commonly four basal teeth, with either the second or third from the base frequently reduced in size. As body size decreases the common basal tooth number becomes three and then two; in the latter case the median tooth is frequently reduced. Superimposed on this allometric variation is the frequent, non-allometric loss of the second intercalary tooth. Clypeus with a well defined median carina, which tends to become obsolescent in small workers. Anterior border of median clypeal lobe broadly and evenly rounded. Head tending to be more massive relative to body than in all other members of the genus with the exception of *L. brunneus.* Color highly variable, from straw yellow to dark yellowish brown. Minor workers are nearly aways clear yellow, medias show various degrees of light infuscation, and very large workers (found in northern Eurasia only) are often deeply infuscated.

Male. Mandible form highly variable, ranging from the presumably primitive *sitkaensis* type to the *niger* type. The variation is partly allometric, i.e. the largest males usually have the *sitkaensis* type, while the smallest males always have the *niger* type or some degenerate modification of it.

GEOGRAPHIC VARIATION. *Forested eastern United States.* Throughout most of the forested portion of the eastern United States, *flavus* occurs sympatrically with the closely related species *nearcticus.* Within this range it consistently exhibits a set of characters which sharply distinguish it from *nearcticus* and set it off, at least statistically, from other *flavus* populations in North America and Eurasia. These characters, described in relation to *nearcticus*, can be summarized as follows:

(1) *Flavus* has a much shorter scape length; the SI-HW regression zones of the two species are well separated (Fig. 11).

(2) *Flavus* has a larger ommatidium number relative to HW; the regression zones of the two species are separate despite the fact that this is a very variable character (Fig. 11).

(3) *Flavus* has a head shape reminiscent of *L. brunneus:* in full face it is broader and tends to narrow more anterior to the eyes, while the mandibles are shorter, more incurved, and inserted closer to the midline. Of 39 series examined for this character, 34 showed the head shape just described and 5 were judged as intermediate to *nearcticus. Nearcticus* is more reminiscent of *L. niger:* the head is subquadrate, with well spaced, "typical" mandibles.

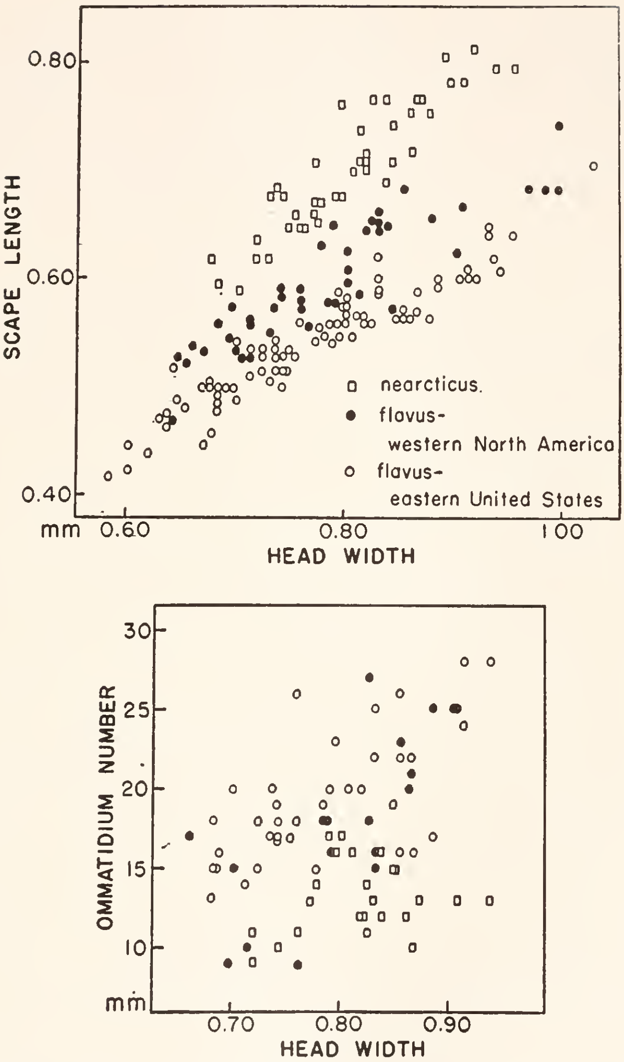

Fig. 11. Differential worker allometry in *L. nearcticus* and two geographic samples of *L. flavus*. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

(4) *Flavus* is more polymorphic, i.e. shows greater intranidal size variation. More than 90 per cent of *flavus* colonies were judged by the naked eye as feebly polymorphic, while the great majority of *nearcticus* colonies were judged as monomorphic.

(5) The palpal character previously described as diagnostic for *flavus* tends to be exaggerated in this population by a further shortening of segment VI relative to V. Thirty out of 34 nest series examined for this character contained at least some individuals with VI distinctly shorter than V.

(6) There is a tendency in *flavus* for a thinning of the cephalic pubescence. In more than 80 per cent of *nearcticus* nest series the margins of the head viewed in full face are covered with short, predominantly subdecumbent to erect pubescence dense enough to give a furry appearance. In *flavus* only 2 out of 11 series examined for the character showed this condition; 5 had the same type of pubescence but much sparser, so that stretches of the margin were nearly bare of it; 4 series were judged intermediate in the character.

(7) The queens of *flavus* are consistently larger. Since the head broadens allometrically with respect to the remainder of the body, this difference is best expressed in terms of the HW-thorax width relationship (Fig. 12).

Western North America. In the area encompassing southwestern Canada, Idaho, Washington, California, Arizona, and Colorado, where *nearcticus* is rare or completely absent, all of the characters above break down to some degree and the population of *flavus* converges toward *nearcticus*. Intermediate as well as extreme conditions occur in various combinations.

(1) The SI regression zone shifts upward to lie in an intermediate position between those of the eastern *flavus* and *nearcticus* (Fig. 11).

(2) The variability of the ommatidium number greatly increases, so that the broadened regression zone overlaps the eastern *flavus* and *nearcticus* zones (Fig. 11.).

(3) The *nearcticus* head shape comes to preponderate over that characterizing the eastern *flavus*. Of 21 series examined, 11 had the *nearcticus* head shape, 4 the head shape of the eastern *flavus,* and 6 were judged intermediate.

(4) Worker polymorphism becomes less common. Less than 50

per cent of the nest series were judged polymorphic with the naked eye.

(5) Maxillary palp segment VI elongates relative to segment V. Eighteen series examined had VI as long as V, whereas only 9 had VI shorter than V.

(6) The average density of cephalic pubescence increases. Of 22 nest series examined, 8 were similar to the typical *nearcticus*

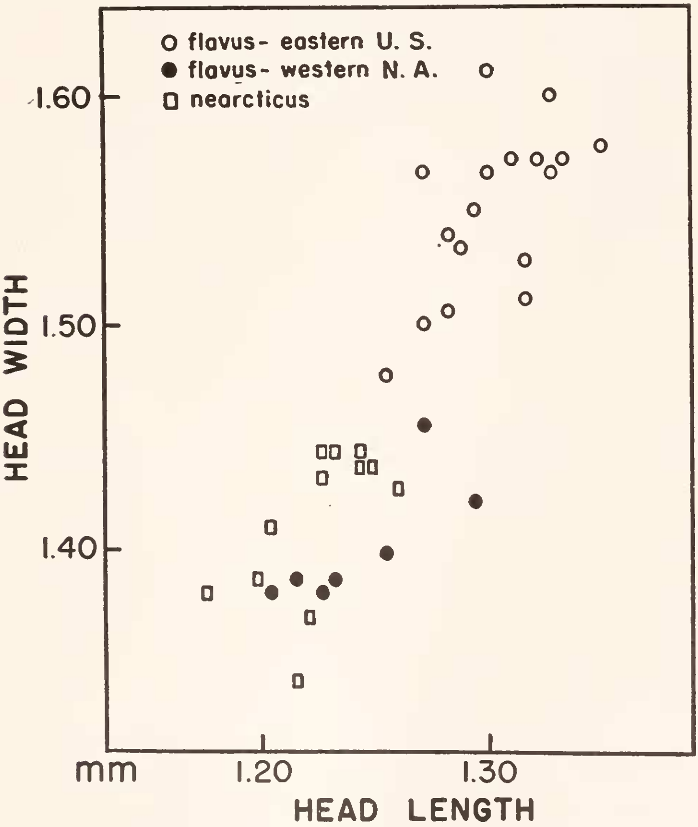

Fig. 12. Queen size variation and head length-head width allometry in *L. nearcticus* and two geographic samples of *L. flavus*. Further explanation in the text. Nest series chosen at random; no more than two queens per series were measured.

condition already described, 7 were similar to the eastern *flavus* condition, and 7 were judged intermediate.

(7) The queen size range decreases to about that of *nearcticus* (Fig. 12).

The picture of geographic variation in North America is an extraordinarily deceptive one. Lining up individual series in terms of character combinations, as I did at first, one easily gains a picture of two sympatric species in eastern North America and a single highly variable population, apparently of hybrid origin, in western North America. This impression is strengthened by the fact that the characters involved assort themselves independently in the western population. In fact, they occur in almost completely random combinations to produce what Anderson (1951) would call "discordant" variation and in higher plants at least associate with interspecific hybridization. The conclusion might be reached in this case that two sympatric species maintain themselves apart over a broad area in the east but have intergraded completely in an adjacent, equally broad area in the west. Such an anomalous situation is not without precedent in taxonomic literature. It has been described in Asiatic butterflies of the genus *Karanasa* (Avinoff and Sweadner, 1951), and for Chinese composites of the genus *Ixeris* (Stebbins, 1950).

Detailed analysis has revealed that this explanation is not the correct one for *Lasius flavus*, however. The clue which led to the alternative explanation, that the western population is a highly variable, but nevertheless pure *flavus* population, came from the SI and palp characters. Unlike the other characters, the SI remains relatively constant in the west, despite the fact that its regression zone is intermediate between the eastern *flavus* and *nearcticus*. One does not find the great spread in variability ordinarily encountered in introgressive hybridization. The palp character presents even more suggestive evidence. Although it converges away from the eastern *flavus* toward *nearcticus*, it converges only up to a point, and it is the only character of the assemblage which preserves a discontinuity. On the basis of the palp character by itself it appears that the western intermediate population is composed almost entirely of *flavus*.

This conclusion is supported by the fact that the southern European population of *flavus* is very close to that in western North America and varies almost as randomly. Were the western North

American population to be considered as having originated through interspecific hybridization, then the southern European population would have to be explained as a migratory extension of the North American population. This is, on any grounds, a most unlikely hypothesis, particularly in view of the fact that most of the "hybrid" variability is still preserved half way around the world from the point of contact between the two "parents".

The western population was finally proven to be *flavus* by an

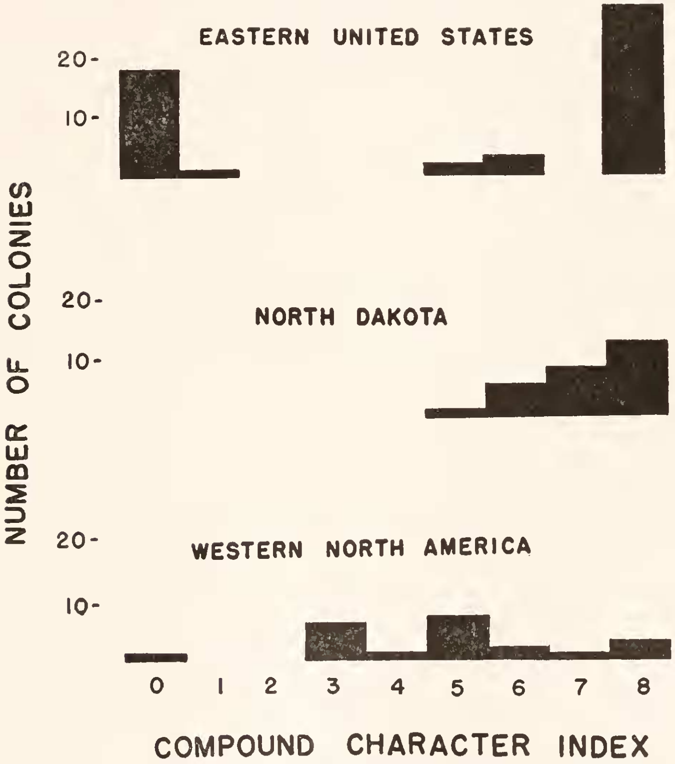

Fig. 13. Frequency histograms of the compound character index of *L. nearcticus* (0-1) and *L. flavus* (3-8) in three geographic samples, illustrating the presumed effect of interspecific competition on geographic variation in the latter species. Further explanation in the text.

analysis of material from many localities in North Dakota, which state includes in its eastern half the transition belt between grassland and deciduous forest; this belt presumably carries the western outliers of the *nearcticus* population. If all of the material from the state is treated as a unit, *flavus* is caught in the very process of shifting from the divergent eastern condition to the more *nearcticus*-like western condition. This population is intermediate between the eastern and western populations when all of the characters are taken together, and it does not exhibit any feature of variation which would indicate hybridization with *nearcticus.*

I have illustrated this remarkable geographic variation in Figure 13 by means of a ''compound character index'', which is identical to the ''hybrid index'' of Anderson (1949), except that species convergence, and not hybridization, is involved. In this graph, typical *nearcticus* characters are each given a score of 0, typical eastern *flavus* characters 2, and intermediate characters 1. The four characters most consistent in the eastern population are used: maxillary palp, scape index, ommatidium number, and head shape. Completely typical *nearcticus* nest series score a total of 0 and completely typical eastern *flavus* 8, with the various ranks of intermediates falling in between.

It is my opinion that competition with *nearcticus* is the major influence effecting this variation in North America. Across Eurasia and western North America *flavus* is mostly intermediate in morphology between the two extreme forms, and in several of the important characters it overlaps *nearcticus* broadly; it is consistently different from *nearcticus* only in the palp character. In the forests of eastern North America it meets *nearcticus* and immediately diverges from it in six additional characters.

It is a well known principle of ecology that two closely related species can succeed in the same geographic area only if they show some ecological difference which prevents their coming into direct and absolute competition. Expressed in another and perhaps more appropriate way, it is to be expected that any ecological difference of two sympatric series will be to their advantage and will be selected if it has a genetic origin (Mayr, 1949a). Increased ecological divergence resulting from selection can be expected in turn to have some collateral effect on the morphology of the species involved. This is the process which I believe has been operative in the profound morphological changes in the eastern North American *flavus*.

There can be little doubt that *flavus* and *nearcticus* are ecologically different where they occur together. Of nine eastern *flavus* collections for which I have data, seven were taken in what may be collectively called open dry woods and two in open moist woods. Of eleven *nearcticus* collections, three were taken in open moist woods and eight in dense moist woods. *Flavus* seems to be able to thrive in bare or poorly covered earth, while *nearcticus* is mostly limited to earth with thick litter and humus cover. There is little information available to tell us whether the western population of *flavus* shows the expected overlapping ecological range. I found this ant abundant on the eastern slopes of the Sierra Nevada, in the vicinity of Yosemite Valley, nesting mostly in open conifer forest with relatively dry soil but under a wide variety of shade conditions. There were few moist woodland situations available at the elevations at which *flavus* occurs. In Europe *flavus* favors open situations but also occurs in moist woodland (see under Ecology).

Maritime Canada. Flavus from this area, roughly north of the 45th parallel, do not seem to conform well with the remainder of the eastern population. Series from Pleasantfield and North Brooksfield, Nova Scotia, and Penobsquis, New Brunswick, have intermediate scape indices. Another series from Pleasantfield has small, "*nearcticus*" eyes. Significantly, *nearcticus* is not known to occur this far north.

Aberrant North American series. Seven nest series encountered among the North American material have presented difficulties in species placement by the palp character. A series of *nearcticus* from Boston, Mass. (W. M. Wheeler leg.; MCZ) has one individual in five with segment V as long as segment VI, the *flavus* condition; another series, from Blind River, Ont. (Wilson leg.; MCZ), has one individual in four with the same condition. Series determined as *flavus* from Garrison, McClean Co., N. Dak. (R. P. Uhlmann leg.; G. C. Wheeler Coll.) and Divide Co., N. Dak. (2 series, J. David leg.; G. C. Wheeler Coll.) have single individuals with segment VI longer than segment V on one palp. In these several cases there is no evidence that hybridization has played a part; all involve single aberrant individuals from otherwise normal nest series. The following two cases are somewhat more difficult to explain. A series from Tar Island, Rockport, Ont. (W. S. Creighton leg. and Coll.) has *nearcticus* palps, intermediate head shape and scape index, and *flavus* eyes. A second series from nearby Buck Island (Creighton) has *nearcticus* palps, intermediate head shape and scape index, and *nearcticus* eyes. Both of these series have been determined tentatively as aberrant *nearcticus;* perhaps they represent a divergent trend in this species at the northern periphery of its range.

Concordance of character variation in North America. As described above, the combination of characters marking the eastern population of *flavus* seems to be closely associated with the distribution of *nearcticus;* they are rapidly modified when *nearcticus* is left behind at the edge of the deciduous forest. The four characters used in the compound character index of Figure 13 exist in the eastern *flavus* condition in a series from Devils Tower, Wyoming (Creighton leg. and Coll.), which is the westernmost known locality for *nearcticus.* They also exist in a series from Gregory Canyon, Boulder, Colo. (Creighton leg. and Coll.) and San Geronimo, N. Mex. (M. Cooper leg.; MCZ), which two localities are conceivably within the range and ecological influence of the *nearcticus*-like species *fallax,* although there is an admitted danger of overstretching a point by bringing this species into the discussion.

The shift of characters in *flavus* from east to west is partly observable in the North Dakota series (mostly G. C. Wheeler Coll.). In this area these characters are really discordant, in that some have been observed to shift to the western trend while others have not. Specifically, if the North Dakota series are treated as a unit (they are too incomplete to show trends within the state), they resemble the western population in queen size and worker palp character and the eastern population in worker eye size and head shape, but show a highly variable mixture of low and intermediate scape indices.

Northern Europe. In Britain, Scandinavia, France, Benelux, and Germany, judging from several dozen series examined, the workers average larger in size than elsewhere and are much more polymorphic, i.e. show greater intranidal size variation and attain larger maximum size. The size frequency curve of a single Scottish nest series (Fig. 14) shows a trend toward bimodality, a characteristic of primitive types of worker polymorphism in general and the most extreme development of this phenomenon in the genus. In addition, these northern series have greater relative eye size and higher scape indices than any other populations. The SI regression zone, in fact, is nearly coincidental with that of *nearcticus*. Queen size is small, closer to the western North American population than to the eastern.

Central Europe and the Mediterranean perimeter. Abundant material, primarily from Italy, Yugoslavia, and North Africa, shows greatly decreased polymorphism, along with diminished relative eye size. Abundant material from Switzerland is clearly intermediate in all three characters, showing the extreme as well as the intermediate conditions in various combinations.

Eastern Asia. Specimens from this area closely resemble the northern European form. Workers from Mt. Akagi (Akagisan), Honshu (MCZ); Nikkō, Honshu (E. Silvestri leg., MCZ; H. Okamoto leg. and Coll.); and Hirooka, Shikoku (Okamoto leg. and Coll.) are long-scaped and large-eyed. Workers from Miao T'ai Tze, Shensi, China (W. L. Brown leg.; MCZ) are long-scaped and small-eyed. Queens from Tokyo (L. Gressitt leg.; MCZ) have HW's of 1.41, 1.44, and 1.47 mm., and a queen from

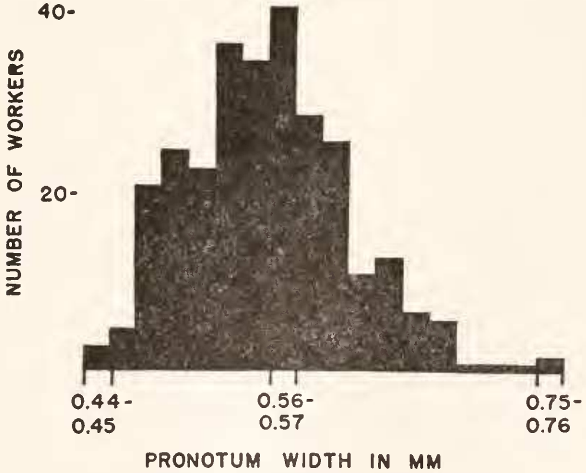

Fig. 14. Size frequency distribution of the workers of a single nest series of *L. flavus* from Kilchattan Bay, Bute, Scotland. Note the skewness characteristic of the early phylogenetic stages of worker polymorphism.

"Eastern Tomb" (Nanking?) (Chi Ho leg.; MCZ) has a HW of 1.42 mm., all consistent with the European population.

Racial divisions. For the benefit of those who insist on applying trinomens to different segments of the population, I believe it is safe to say that the only workable division which can be made is between the eastern North American population ("*flavus brevicornis*") and the rest of the species ("*flavus flavus*"). The western North American population is exceedingly close to that of Italy and North Africa, differing only in having larger eyes, longer scapes, a slightly greater tendency toward polymorphism, and a frequent occurrence of the "*nearcticus*" head shape (absent in Europe); there is wide overlap in these characters admitting of no subspecific division by conventional standards (cf. Mayr, Linsley, and Usinger, 1953). The southern and northern European segments differ by several characters, including degree of polymorphism, scape length, and eye size, but there is a wide zone of transition between them, and, more important, the western North American population falls intermediate between the two in every character.

DISTRIBUTION. *L. flavus* has a very wide range through Eurasia and North America, exceeded within the genus only by that of *L. alienus.* According to Donisthorpe (1927) *flavus* occurs throughout England and reaches into southern Scotland; I can supply the following supplementary records from southern Scotland: Aberfoyle (MCZ); Kilchattan Bay, Bute (M. V. Brian leg.; MCZ); Glen Luss, Dumbarton (Brian leg.; MCZ); Ballochraggen, Stirling (Brian leg.; MCZ); North Berwick (Brian leg.; MCZ). In Ireland, according to O'Rourke (1950) *flavus* reaches northward to Malin Head on the coast and to south of Dublin inland. Holgersen (1944) has taken it in Norway north to Vågå, Opland. Forsslund (1947) has found it in southern, central, and eastern Sweden north to Västerbotten Province and southeastern Lappland; I have determined material in his collection originating from as far north as Luleå, Norrbotten. The species reaches southern Finland (Helsinki; Forsius leg.; MCZ) and probably extends eastward across the northern part of European Russia. The large amount of material I have examined from western Europe, coupled with numerous local faunal reports in the literature, indicate that *flavus* is abundant from southern Scandinavia as far south as the mountains of central

Italy. It occurs in northern Spain (Menozzi, 1922), and I have seen material from southern Italy (Sambiase, Calabria; MCZ), numerous localities in northern and central Yugoslavia (all MCZ), Albania (Tomorica; Ravasini and Lona leg.; MCZ), and Lebanon (mountain above Kammouha Plain, 1500 meters, winged queens and males; K. Christiansen leg.; MCZ). I have determined series from the following North African localities: Azrou, Morocco (W. M. Wheeler leg.; MCZ); Tachdirt, Morocco (R. Koch leg.; MCZ); Terni, Oran, Algeria (*myops* Forel syntypes). So far as I know *flavus* has never been taken in the Balearics, Canaries, Azores, or on Madeira. It occurs in the Caucasus (Schneider leg.; MCZ). According to Karawajew (1931) it occurs fairly far north in Siberia, reaching the Tomsk and Yenisei Districts, the Akmolinsk region, the Yakutsk District (north to Ust Kut), and Kamchatka. One gains the impression from the literature that *flavus* is rare or absent around most of the Tibetan Plateau. Kusnetzov-Ugamskij (1929a) states that it occurs in the Tien Shan, but is scarce there and limited to high elevations. Menozzi (1939) did not find it in the substantial collections of the genus made in the Karakoram and western Himalayas by the Duca di Spoleto expedition. Eidmann (1941) found a single series of "*myops*" in the collections of the Brooke Dolan expedition to the eastern rim of the Tibetan Plateau, but this may well be *talpa* Wilson instead of *flavus*. The several eastern Asiatic records verified during the present study have already been presented in the section on geographic variation.

In North America *flavus* is distributed similarly to *L. umbratus*, being abundant through most of the eastern half, declining in the southern Rockies, and becoming rare or absent in the northern Rockies and Pacific Northwest. It differs from *umbratus* in being abundant in the Sierra Nevada of California. I have compiled the following records from southeastern Canada: Blind River, Ont. (E. O. Wilson leg.; MCZ); Ottawa, Ont. (USNM); Hull, Quebec (W. M. Wheeler leg.; MCZ); Penobsquis, New Brunswick (C. A. Frost leg.; MCZ); Pleasantfield and North Brookfield, Nova Scotia (W. H. Prest leg.; MCZ). Numerous field observations by the present writer, local faunal studies published by others, and the abundance of material in collections suggest that *flavus* is a common species throughout the eastern United States south to the mountains of North Carolina and

Tennessee. It is rare in the Gulf States; I have collected it at Peterson and Brookwood, Tuscaloosa Co., Ala. (MCZ), while Smith (1931) has recorded it from Ripley, Tippah Co., Miss. Westward, Buren (1944) found it common in Iowa, while the collections of G. C. Wheeler and his students contain numerous series from over all of North Dakota.

I append the following western records, exclusive of North Dakota, compiled during the present revision. SOUTH DAKOTA: Pierre (W. M. Wheeler leg.; MCZ); Hot Springs, Fall River Co. (MCZ); Hill City (T. Ulke leg.; USNM). WYOMING: Devils Tower, Crook Co. (W. S. Creighton leg. and Coll.). SASKATCHEWAN: Farewell Creek (MCZ). ALBERTA: Banff (subsp. *claripennis* Wheeler syntypes). IDAHO: Bloomington Ridge, Wasatch Range, 9000 feet (B. Malkin leg. and Coll., MCZ). COLORADO: Gregory Canyon, Boulder (Creighton leg. and Coll.); Topaz Butte, Florissant, Teller Co., 9000 feet (W. M. Wheeler leg.; MCZ); Cheyenne Canyon, Colorado Springs (MCZ); Canon City, Fremont Co. (Schmitt leg.; MCZ); Creede, Mineral Co., alate queen (MCZ). NEW MEXICO: between Raton Pass and Raton, Colfax Co., 7100 feet (A. C. Cole leg. and Coll., MCZ). ARIZONA: Soldier's Camp, Santa Catalina Mts., 7700 feet (L. F. Byars leg. and Coll., MCZ); Mt. Lemmon, Santa Catalina Mts., 9150 feet (W. M. Wheeler leg.; MCZ). NEVADA: Lehman Caves, Mt. Wheeler (Creighton leg. and Coll.). CALIFORNIA: Sequoia National Park (Creighton leg. and Coll.); Kings Canyon National Park (J. H. Eads leg.; MCZ); Dalton Creek, Fresno Co., 4800 feet (H. Dietrich leg.; specimen lost); Camp Curry, Yosemite National Park, 4000 feet (subsp. *microps* Wheeler syntypes; also Wilson leg.; MCZ); Mariposa Grove, Yosemite National Park, 6500 feet (Wilson leg.; MCZ); 14 miles west of Dardanelle, Tuolumne Co., 6500 feet (Wilson leg.; MCZ); Twain-Harte, Tuolumne Co. (F. E. Blaisdell leg.; CAS); Lake Tahoe (*helvus* Cook types; also W. M. Wheeler leg., MCZ). OREGON: Mt. Hood, 6500 feet (Cole Coll.). WASHINGTON: Cle Elum, Kittitas Co. (T. Kincaid leg.; Cole Coll.); Pullman (W. M. Mann leg.; MCZ).

ECOLOGY. The nesting habits and habitat preferences of *flavus* are subject to marked geographic variation. In Germany, Gösswald (1932) found the species to be highly adaptable, occupying moist forest floors, forest borders, hedgerows, grassy paths, and sparsely vegetated wasteland. It is able to penetrate into cultivated areas but does not nest in gardens. In a random field sample, Gösswald recorded 835 colonies under stones, usually in dry situations, 300 in mounds, mostly in meadows, and 30 in dead tree trunks in woodland. The mounds reach their largest size in swampy areas, and may exceed 60 cm. in height. Gösswald judged this species to be more adaptable, although not more abundant, than *L. niger*. He encountered 6 colonies that he determined as "*myops*", all under rocks in open, dry ground. It sounds likely that these were depauperate colonies living in a habitat affording only marginal existence.

Many other authors have made similar observations concerning the diverse nesting habits of *flavus* in northern and central Europe. O'Rourke (1950) found it in Ireland mostly in dry, sunny situations with fine soil, but never encountered it in marshes or in rotting wood in forests. Skwarra (1929) found it to be a very successful ant in the Zehlau Moor of East Prussia, exceeded in abundance there only by *L. niger;* she notes the general preferences of this species for open, moist, grassy land, in fields, marshes, along the shores of inland lakes and ponds, and on riverbanks.

The mounds which the European *flavus* builds have been described in the literature many times. In Switzerland they occur mostly on eastern and southern mountain slopes, tending to increase in height and size with elevation (Wheeler, Forel, *et al.*). They are typically elongate in shape under these conditions, with the long axis east-west and the east face precipitous. According to Linder (1908) this peculiar shape is caused by the ants inhabiting and building only in the east end of the mound.

In southern Europe, in the lowlands at least, the mound-building habit is lost, and the species nests almost exclusively under stones. Zimmermann (1934), for instance, found it limited to this latter nesting site in the islands around the Quarnerolo. At Miao T'ai Tze, Shensi, China, W. L. Brown (pers. commun.) found *flavus* nesting under stones. This is the only type of nesting site I encountered in several dense populations in the Sierra Nevada of California, and is by far the predominant type through the eastern U.S. I do not know of any cases in North America of *flavus* constructing mounds in open soil.

European observers are in agreement that *flavus* is completely subterranean. Its mounds ordinarily lack external openings and workers are rarely seen above the ground. In Ontario and California I watched for signs of activity around *flavus* nests at night, but was never rewarded with the sight of a foraging worker. It has been generally assumed that the main food source of this species consists of the secretions of Homoptera maintained in the nests (cf. Eidmann, 1926), but food habits have never been well investigated. Indeed, I have only occasionally found evidence of any food source, including Homoptera, in a number of nests I have excavated, although workers and brood were turned up in abundance. The utilization of some amount of insect food seems likely. Donisthorpe (1927, p. 258) mentions the presence of insect remains in *flavus* galleries under stones, and Richards (1953, p. 128) has observed *flavus* workers dismembering a caterpillar on top of a mound.

The mass of published data on nuptial flights by this species in Europe has been well summarized by Donisthorpe (1927). The flights occur in the late afternoon from July to September and predominantly in August. They are often concurrent with flights of *L. niger*. Winged forms are found in the nests from June to October. I have seen *in nido* North American collections of winged forms ranging from July 21 (Penobsquis, New Brunswick) to August 30 (Rochester, New Hampshire).

SYNONYMY. *Lasius brevicornis* Emery. Lectotype by present selection, a queen in the MCZ labelled "Georgetown, D. C., Coll. Hill, Aug. 10, 85, under stone." This specimen is typical for the eastern North American population of *flavus* in head width (1.61 mm.) and in the maxillary palp (segment V longer than VI). A worker syntype in the MCZ from Cuckoo, Va., is typical for the eastern population in all of the characters previously described. This is the available and appropriate name if a trinomen for the population is to be applied at all.

Lasius flavus myops Forel. Lectotype by present selection, a worker in the MCZ labelled "Terni, 9/IV." PW 0.50 mm., HW 0.73 mm., SL 0.59 mm., SI 81, ommatidium number 29 and 26, maxillary palp segment VI as long as V. SI and ommatidium number consistent with the southern European-North African population, but *myops* is not applicable as a trinomen since this population cannot be given subspecies rank even by conventional standards. The simple allometric basis for reduction in eye size in this form was first recognized by Emery (1915), but to van Boven (1951) must go the credit for first demonstrating the relationship by precise measurements.

Lasius flavus myops var. *flavoides* Forel. This is the first name applied to the form intermediate between *flavus* and *myops.* It was characterized as having an ommatidium number of about 30. Syntypes in the AMNH are typical small *flavus* workers.

Lasius flavus var. *fuscoides* Ruzsky. This name was proposed to cover specimens from European Russia, the Caucasus, and Siberia with brown to reddish brown heads and gasters. Although I have little material from this area and no types, I am convinced that *fuscoides* is nothing more than the darker form of major worker which also occurs through the Balkans and western Europe.

Lasius flavus var. *odoratus* Ruzsky. This mysterious variety was based primarily on its odor, said to resemble an ''aromatic geranium.'' In addition, the scale was described as narrower toward the top than in the typical *flavus*, but this is a very variable structure within the species and of dubious taxonomic value. Kuznetzov-Ugamskij (1929a) comments that all of the many series of *flavus* which he collected in the Ussuri region of southeastern Siberia possessed a distinct aromatic odor and could be included in Ruzsky's variety. In tentatively assigning this variety to the synonymy of *flavus,* I must point out that it may represent a distinct cryptic sister species instead.

Lasius brevicornis microps Wheeler. Lectotype by present selection, a worker in the MCZ. PW 0.52 mm., HW 0.77 mm., SL 0.62 mm., SI 81, ommatidium number in both eyes 15. The reasons why this form cannot be upheld even by conventional subspecies standards have already been made clear in the section on geographic variation.

Formicina flava var. *morbosa* Bondroit. The principal characters given for this variety were longer scapes and larger eyes in a small, uniform worker caste. Bondroit thus chose three of the most variable characters in the western European population. There is nothing in the description to indicate that *morbosa* falls outside the normal range of variation of *flavus.*

Lasius umbratus var. *apennina* Menozzi. When, after eight years, Menozzi realized he had determined the *apennina* types to the wrong species, he was hard put to find a character with which to salvage his varietal name. The one he did use, erect hairs present on the tibiae, is an infrequent but normal variation encountered in the western European population.

Lasius umbratus ibericus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.76 mm., HW 1.17 mm., SL 0.92 mm., SI 79. Two additional syntype workers in the same collection were examined. This series is typical *flavus,* possessing characteristic metapleural gland openings (excluding it from *Chthonolasius*), polymorphism, petiolar scale, coloration, pilosity, etc.

Lasius umbratus ibericus var. *sancho* Santschi. This form was described as nothing more than a trivial variant of *ibericus.*

Lasius flavus var. *olivacea* Karawajew. This variety is supposedly distinguished by the possession of a dirty olive-green overtone to the normal color and by slightly broader scapes. I have never seen material fitting this description and suggest synonymy in this case only tentatively.

Lasius helvus Cook. Holotype and one paratype in the Cook Collection, one paratype in the MCZ. Through the courtesy of Dr. Cook I have been allowed to examine all three of the type specimens. This species is a clearcut synonym of *L. flavus* and does not deviate in any way from the western North American population. To avoid possible confusion in the future I must point out that the figures accompanying the original description are badly in error with respect to scape length, eye size, and alitrunk shape. Also, the size (PW 0.47 mm.) is not unusually small, as was claimed by Dr. Cook.

LASIUS FALLAX Wilson, new species

(Subg. *Cautolasius*)

DIAGNOSIS. A population inhabiting the Rocky Mountains and Great Basin from Idaho and Montana south to southern Arizona, almost exactly intermediate in each of the critical diagnostic characters separating *flavus*, *nearcticus* and *talpa.* Because it is parapatric with *nearcticus,* the possibility exists that it represents a western variant of that species, but for several reasons to be given later, it has been treated herein as a distinct species.

Worker. (1) Outer surfaces of the tibiae with numerous standing hairs prominent above a dense ground pubescence. Scapes with dense standing pubescence grading into hairs of intermediate length (¼-½ × as long as the maximum scape width) but with few or no outstanding hairs along the plane of count.

(2) Relative lengths of the two terminal segments of the maxillary palp very variable within individual nest series, grading from the *flavus* condition (segment V equal to or longer than segment VI) to the *nearcticus* condition (segment V shorter than segment VI). The *flavus* condition usually preponderates, and the *nearcticus* condition may be altogether absent in any single nest series.

(3) The allometric regression zones for both ommatidium number and scape length relative to head width appear to be exactly consistent with those for the western North American population of *flavus,* which is intermediate between *nearcticus* and the sympatric eastern population of *flavus.* The minimum recorded ommatidium number is 12, higher than in the majority of *talpa* series.

Queen. Appendage pilosity as in worker. Terminal maxillary palp segments as in *flavus,* varying within single nest series from segments V and VI equal in length, to V longer than VI. Size variation similar to that of *nearcticus* and western North American-Eurasian *flavus;* HW 1.38-1.55 mm. Color similar to *flavus,* darker than *talpa.*

Male. At least 2 or 3 and usually more than 6 standing hairs along the outer lateral femoral surfaces; in *nearcticus* rarely more than 1 or 2 and usually none. Mandible form varying as in other *Cautolasius.*

HOLOTYPE. A worker in the Creighton Collection selected from a series collected at Bassets Springs, Uinta Mts., Utah, with associated winged queens and males (W. S. Creighton leg.). PW 0.50 mm., HW 0.72 mm., SL 0.57 mm., SI 79, ommatidium number 19 and 27. Paranidotypes are in the MCZ.

FURTHER DESCRIPTION. *Worker.* PW range 0.44-0.70 mm., maximum intranidal range 0.44-0.56 mm. (Hartzel, Colo.) and 0.49-0.67 mm. (Kaibab Nat. For., Ariz.). Head shape usually more like that of *nearcticus* than *flavus,* i.e. subquadrate with widely spaced mandibles; intermediate in the Monticello, Utah series. Cephalic pubescence as in *nearcticus.* Mandibular dentition similar to *nearcticus,* showing part of the *flavus* variation; two basal teeth always present, occasionally with a third, intercalary tooth, and a second intercalary tooth present in all specimens examined. Color of body and appendages medium yellow to very light yellowish brown, head often a shade darker than the rest of the body.

Male. Subgenital plate of male from Lost River Range, Idaho, subquadrate, with a single prominent median setiferous lobe. Lacking the extended posterolateral flanges of *talpa.*

GEOGRAPHIC VARIATION. The known range of *fallax* overlaps that of *flavus* in Washington, Idaho, central Colorado, and northern Arizona, and it is almost perfectly contiguous with that of *nearcticus.* The possibility therefore exists that *fallax* represents a population of *nearcticus* which has shifted in its morphology in a direction toward *flavus,* just as *flavus* shifts toward *nearcticus* in North Dakota and the Far West. This possibility is strengthened by the fact that the *fallax* pilosity character is weakest, and may even be considered intermediate to *nearcticus,* in the two series (Glacier Nat. Park and Hartsel) taken closest to the known *nearcticus* range.

Nevertheless, I have decided to regard this population as a distinct species for the following reasons. It has not been established in the first place that *fallax* is not really a population of *flavus,* since they have never been taken together in the same immediate locality, and they are perhaps even closer to one another morphologically than *fallax* and *nearcticus.* To include *fallax* in *nearcticus* on the basis of available material would be an arbitrary step which would greatly complicate the already confusing diagnosis of *nearcticus;* the reason for this is that the one pristine *nearcticus* character, that of the relative lengths of the terminal maxillary palp segments, breaks down in *fallax.* Also, while the Glacier National Park and Hartsel series approach *nearcticus* in pilosity, they do not approach it in the palpal, scape, and eye characters; all of the *fallax* series are consistent in these three characters. Future collecting may prove me wrong, but it appears at the present time that the most stable and practical classification will be one in which *fallax* is segregated as a full species.

DISTRIBUTION. Over 200 workers, 16 queens, and 13 males were examined from the localities listed below. Except for the Washington and Glacier National Park series, all collections were made by Dr. W. S. Creighton, and the bulk of the type material is in his collection.

WASHINGTON: Huntsville, Columbia Co. (A. C. Burrill leg.; MCZ); Kamiak Butte, Palouse, Whitman Co. (A. C. Burrill leg.; MCZ). IDAHO: Double Springs Summit, Lost River Range, winged queens and males VIII-22-1933. MONTANA: Lake McGregor, Flathead Co.; St. Marys Entrance, Glacier Nat. Pk. (E. O. Wilson leg.; MCZ). WYOMING: 20 miles east of Moran. COLORADO: Hartsel, Park. Co. UTAH: Bassets Springs, Uinta Mts. (holotype nest series); Deep Creek, Uinta Mts.; Warner Ranger Station, La Sal Mts., males VII-19-1933; Monticello, Blue Mts., winged queens and males VII-30-1933. ARIZONA: Kaibab National Forest, Grand Canyon.

ECOLOGY. The Glacier National Park series was taken from a populous colony nesting under a stone in a clearing in a pine-fir forest at about 5000 feet. *Lasius sitkaensis* was abundant in the same immediate area, under stones in clearings as well as in rotting logs in the forest. *L. crypticus* also occurred in the clearings under stones.

Lasius nearcticus Wheeler

(Subg. *Cautolasius*)

Lasius flavus nearcticus Wheeler, 1906, Psyche, **13**: 38–39; worker; original description. Type locality: Illinois, by selection of Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 422.

DIAGNOSIS. *Worker.* (1) Segment VI of the maxillary palp distinctly longer than segment V.

(2) Scape long, always surpassing the occipital border by a considerable margin, the SI-HW regression zone well above those of the majority of series of other *Cautolasius* with the exception of the northern Eurasian population of *flavus* (Fig. 11).

(3) Eyes small relative to head size, ommatidium number usually 9 to 17, but still averaging larger than in *talpa* (Fig. 11).

(4) Differing from the sympatric eastern North American population of *flavus* by a number of other distinctive characters

which break down in the allopatric western North American and Eurasian populations of *flavus* (see the section on geographic variation in that species).

Queen. (1) Usually sharing the maxillary palp character of the worker. Single, exceptional, individuals from nest series from Catawba, Ohio (M. Amstutz leg.; Talbot Coll. and MCZ) and McGregor Lake, Quebec (F. J. O'Rourke leg.; MCZ) have segment V equalling segment VI in length on one side only.

(2) Differing in size from the sympatric eastern North American population of *flavus* (see under *flavus*).

Male. The diagnostic palpal character of the worker and queen is not shared by this caste; segment V is usually as long as VI and occasionally longer, the relative lengths showing considerable intranidal variability. The only possible distinctive character I have encountered is in the subgenital plate. In several *nearcticus* series examined it is shaped like a rectangle bent posteriorly, so that the anterior border is evenly convex and the posterior border evenly and deeply concave. The posteromedian setiferous area tends to be less prominent than in other *Cautolasius* and is one- or two-lobed. The subgenital plate of *flavus* is typically subquadrate in shape, although series from the Chilhowee Mountains of Tennessee are indistinguishable from *nearcticus,* while the plate figured by Clausen (1938) from Zurich is intermediate.

TYPES. The location of Wheeler's syntypes is unknown. The original description mentions workers from Illinois, Massachusetts, Connecticut, New York, and New Jersey, and it is possible that determined series in the MCZ from Colebrook, Conn. (Wheeler) and Woods Hole, Mass. (A. M. Field) were among the ones originally studied. For no stated reason Creighton (1950) selected Illinois as the type locality, even though no Illinois material is in the determined Wheeler collection. Since definitely authentic material may yet be discovered, it would be very unwise at this point to recognize any specimens as syntypes and to select a lectotype. Fortunately, Wheeler's description of the worker, his later determination of material in the MCZ, and his comments on the ecology ("only in damp soil in shady woods") leave little doubt that the present assignment of the name is correct.

FURTHER DESCRIPTION. PW range 0.45-0.64 mm., maximum intranidal size variation 0.45-0.58 mm. (Gibraltar Island, Ohio; M. Amstutz leg.; Talbot Coll.). Apparently the least size-variable and most monomorphic of the four better known *Cautolasius* species. Mandibular dentition showing part of the variation seen in *flavus:* two well-developed teeth present and often a third, intercalary tooth in addition; the regular second intercalary tooth present in all specimens examined. Head covered with a dense ground pubescence, which obscures the margins of the head viewed in full face; this character also occurs in *talpa* and *fallax* but is only occasional in *flavus.* Color pale to medium yellow, the gaster often lighter than the alitrunk and the alitrunk lighter than the head; averaging and ranging overall lighter than other members of the subgenus.

Male. Mandible form showing the same extreme range of variation as in *flavus*, from the "*sitkaensis* type" to the "*niger* type."

DISTRIBUTION. This species is common throughout most of the forested area from southeastern Canada to the southern Appalachian mountains. It is occasional as far west as South Dakota and Wyoming. Specific Canadian records accumulated during the present study are as follows: Kingsmere, Que. (W. M. Wheeler leg.; MCZ); Lake McGregor, Que. (F. J. O'Rourke leg.; MCZ); Hull, Que. (Wheeler leg.; MCZ); Arnprior, Ont. (C. Macnamara leg.; USNM); Tar Is. and Buck Is., Rockport, Ont. (W. S. Creighton leg. and Coll.; tentative determination, see under geographic variation in *flavus*). Several collections by A. C. Cole, A. Van Pelt, and myself show that *nearcticus* is fairly common at intermediate elevations in the southern Appalachian mountains of extreme western North Carolina and eastern Tennessee. It has never been taken in the Gulf States, with the single possible exception of an old series marked "Tex." in the USNM. Following are given the westernmost records verified during the present study: Ames, Iowa (W. F. Buren leg.; USNM); Palo Alto Co. and Dickinson Co., Iowa (R. L. King leg. and Coll., MCZ); Deadwood, S. Dak. (E. and G. C. Wheeler leg.; G. C. Wheeler Coll.); Hill City, S. Dak. (W. S. Creighton leg. and Coll.); Devils Tower, Wyo. (Creighton leg. and Coll.).

ECOLOGY. This species is most commonly encountered in dense, moist woodland. Workers and brood are usually found assembled in galleries under rocks and fallen logs, but by digging to the side away from these shelters, one can easily disclose lateral galleries leading off into the open soil, and workers are often turned up by random trenching through the soil.

A nuptial flight involving both sexes was observed by Dr. Mary Talbot (*in litt.*) at Gibraltar Island, Put-in Bay, Ohio, around 5 p.m. on August 26, 1930. I have verified the following *in nido* records of reproductives: Hull, Que., VIII-13-1913 (MCZ); Kingsmere, Que., IX-1-1913 (MCZ); Woods Hole, Mass., IX-23-1901 (MCZ); Arlington, Mass., VIII-30-1952 (E. O. Wilson leg.; MCZ), VII-17-1953 (W. L. Brown leg.; MCZ); E. S. George Reserve, Mich., VIII-23-1953 (M. Talbot leg. and Coll.); Catawba, Ohio, VIII-18-1938 (M. Amstutz leg.; Talbot Coll.); South Bass Island, Ohio, VIII-15-1931 (Talbot leg. and Coll.); Green Island, Ohio, VIII-25-1932 (Talbot leg. and Coll.); Louisville, Ky., IX-3-1950 (Wilson leg.; MCZ); Palo Alto Co., Iowa, VII-30-1946 (R. L. King leg. and Coll.); Dickinson Co., Iowa, VIII-17-1947 and VIII-17-1952 (King leg. and Coll.).

LASIUS TALPA Wilson, new species

(Subg. *Cautolasius*)

DIAGNOSIS. An eastern Asian species best distinguished from other members of the subgenus by its very hairy, small-eyed worker caste.

Worker. (1) Monomorphic to feebly polymorphic. Head shape similar to *nearcticus*, subquadrate with widely spaced mandibles.

(2) Eyes very small, usually with only 6-12 ommatidia and a recorded maximum of 17 (Miao T'ai Tze).

(3) Numerous erect hairs on the scape along the plane of count standing out above the combined ground pubescence and subdecumbent to erect hairs of intermediate length. Standing hairs also abundant on the tibiae. Standing body pilosity in general denser than in other *Cautolasius*.

Queen. (1) Best distinguished from other *Cautolasius* species by the presence of numerous standing hairs on the scape.

(2) Possibly averaging smaller than other *Cautolasius* species: three queens from the holotype nest series have HW's of 1.33, 1.35, and 1.35 mm. respectively.

(3) Body uniformly light brown, overall lighter than in other members of the subgenus.

Male. Lacking a dependable pilosity character; at most two or three erect hairs can be seen on the outer femoral surfaces, a condition probably overlapped by *nearcticus.* The mandibles may have a distinctive shape: the one perfect specimen I have examined, from the holotype nest series, had the masticatory border smooth, concave, and terminating in a sharply angular basal corner, which condition has been encountered elsewhere only in the highly variable *flavus* mandible.

HOLOTYPE. A worker in the Okamoto Collection selected from a series collected at Hirooka, Shikoku, on July 23, 1946, with associated queens and males (H. Okamoto leg.). PW 0.54 mm., HW 0.76 mm., SL 0.60 mm., SI 79, ommatidium number 9 and 10. Paranidotype workers, queen, and male in Okamoto Coll. and MCZ.

FURTHER DESCRIPTION. *Worker.* PW range 0.38-0.60 mm.; maximum intranidal PW range 0.38-0.51 mm. (Yasu) and 0.50-0.60 mm. (Hirooka III-8-1936). SI-HW regression zone high, at lower limit of northern Eurasian *flavus* zone (*q.v.*) and below that of *nearcticus.* Dentition similar in variation to that of *flavus* of comparable size; typically two basal teeth and occasionally a third intercalary one; the second intercalary tooth often dropping out. Terminal segments of maxillary palp apparently varying as in *fallax.* The Hirooka III-8-1936 series contains some workers with VI equalling V and some with VI exceeding V, while all of the Yasu workers have VI exceeding V. Petiole always showing some degree of emargination, although this tends to be feeble in small specimens. Cephalic pubescence as dense as in extreme *nearcticus* (see under discussion of geographic variation in *flavus*). Body and appendages uniformly medium yellow.

Male. Parameres and volsellae resembling those of other *Cautolasius.* Subgenital plate subquadrate, with a single prominent posterior setiferous lobe; posterolateral flanges drawn out laterally and very thin and acute.

GEOGRAPHIC VARIATION. Although available series are far too scanty to judge, it may be significant that the workers with the largest eyes are from the westernmost locality, Miao T'ai Tze.

DISTRIBUTION. A limited series, consisting of a total of 45 workers, 3 queens, and 2 males, was examined from the following localities. KYUSHU: Hikosan (Buzen) (2 series, K. Yasumatsu leg. and Coll., MCZ). SHIKOKU: Hirooka (holotype nest series; also III-8-1936, H. Okamoto leg. and Coll., MCZ); Yasu (Okamoto leg. and Coll., MCZ); Kochi (Okamoto leg. and Coll., MCZ). HONSHU: Tokyo, winged queens IX-1931 (L. Gressitt leg.; MCZ); Ichinomiya (F. Silvestri leg.; MCZ); Kanagawa Pref. (H. Sauter leg.; MCZ); Minoo, Osaka Pref. (M. Azuma leg.; Holgersen Coll.); Arima, near Kobe (Azuma leg.; USNM). KOREA: Pyongyang (Keijo) (Silvestri leg.; MCZ), CHINA: Peking (C. F. Wu leg.; MCZ); Miao T'ai Tze, Shensi (W. L. Brown leg.; MCZ).

ECOLOGY. Dr. W. L. Brown has supplied me with field notes on his Chinese collection. Miao T'ai Tze is located in the Tsinling Shan at an elevation of over 6000 feet. The colony was situated in a small rotting stump on a steep slope in moist, mixed fir-hardwood forest (*Liquidambar, Acer,* and bamboos prominent) about 200 feet above the town. A large colony of *L. flavus* was found under a stone about 400 feet higher in a forest clearing. It is conceivable that *talpa* is the ecological equivalent of the North American species *nearcticus* in that it may tend to replace *flavus* in moister, more densely wooded situations.

LASIUS FULIGINOSUS (Latreille)

(Subg. *Dendrolasius*)

Formica fuliginosa Latreille, 1798, Essai Fourmis France, p. 36; worker, queen, male; original description. Type locality: France.

Lasius fuliginosus var. *nipponensis* Forel, 1912, Ann. Soc. Ent. Belg., **56:** 339; worker; original description. Type locality: Tokyo. NEW SYNONYMY.

Lasius nipponensis, Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18:** 278.

Lasius fuliginosus var. *orientalis* Karawajew, 1912, Rev. Russ. Ent., **12:** 586–587; worker; original description. Type locality: Korea. NEW SYNONYMY.

Acanthomyops fuliginosus capitatus Kuznetzov-Ugamskij, 1928, "Ants of the Southern Ussuri Region" (In Russian), U. S. S. R. National Geographic Society Publications, p. 18; 4 figs. p. 43: worker; original description. Type locality: Okeanskaja Railroad Station, near Vladivostok, Soviet Maritime Territory, by present restriction. NEW SYNONYMY.

Lasius fuliginosus orientalis, Kuznetzov-Ugamskij, 1929, Zool. Anz., **83:** 24. [*nec* Karawajew; objective synonym of *capitatus*, *vide supra*.]

DIAGNOSIS. *Worker.* (1) Head usually deeply concave in full face, the depth of the concavity 0.06 mm. or more except in some series from northeastern Asia (see under geographic variation).

(2) Antennal scapes short-elliptical in cross-section, so that for most of their length the minimum width at any point is 0.8 × the maximum width at that point or greater.

(3) Petiole in frontal view broadest at about the level of the dorsal margin of the anterior foramen, gradually narrowing to the top. The dorsolateral angles broadly and evenly rounded; the dorsal margin narrow, convex to feebly emarginate. In side view the petiole symmetrical, with both faces feebly and evenly convex, tapering together to form a narrow-U-shaped dorsal crest (Pl. 2, Fig. 7).

(4) The hairs of the exposed gastric tergites shorter than in *spathepus* and *crispus*, rarely longer than 0.08 mm. and probably never surpassing the longest hairs of the pronotum. The appendages covered with dense appressed-to-decumbent pubescence but with few or no standing hairs.

Queen. (1) HW 1.41 mm. (Odawara, Japan) to 1.65 mm. (England); see under geographic variation.

(2) Lacking the "beta" characteristics of the *spathepus* queen, i.e. the occipital margin in full face is only weakly concave, the head is about as long as broad or longer, and the mandibles are not exceptionally reduced relative to the remainder of the head.

(3) The entire body, exclusive of the appendages and (in European series) the anterior half of the head, covered with abundant, coarse suberect-erect hairs. In occasional specimens these hairs are rather sparse on the gastrict tergites, but this may be due to wear. The entire body is covered with appressed ground pubescence of varying density which partly obscures the smooth, shining cuticular surface.

(4) Petiolar lateral outline as in worker. Frontal outline typically as in worker and dorsal margin showing same degree

of variation as in that caste; occasionally the broadest level is well above its usual location at the dorsal margin of the anterior foramen.

(5) Median clypeal carina feebly developed (see under *buccatus*).

Male. (1) HW 1.00 mm. (Kiev) to 1.24 mm. (Innsbruck).

(2) Scape short-elliptical to circular in cross-section.

(3) Petiolar outline in side view similar to that of the worker, differing only in being generally thicker. In frontal view the broadest point is at the level of the dorsal margin of the anterior foramen or higher; the dorsal margin is convex in all series examined.

(4) Pygostyle similar to that typifying the subgenus *Lasius:* thumb-shaped, nearly as broad near the tip as at the basal attachment (Pl. 2, Fig. 11). The usual form of the subgenital plate is shown in Plate 2, Fig. 9.

GEOGRAPHIC VARIATION. *The Odawara queens.* The single series of Asiatic *fuliginosus* queens (Odawara, Honshu; M. Kubota leg.; MCZ) I have been able to examine shows several differences from European material that may reflect geographic variation. These queens are smaller, ranging 1.45-1.48 mm. in HW as opposed to 1.62-1.70 mm. for the European series. They have more abundant standing hairs on the anterior half of the head, so that in full face suberect-erect hairs are abundant along the genal outline from the anterior border of the eye to the mandibular insertion, whereas in European material hairs are rare or absent there. The appressed ground pubescence of the body is far denser in the Odawara queens, giving a grey overtone to the body surface at low magnifications. A case may be made in the future for according this form specific status; at present such a move seems inadvisable in view of the fact that the Odawara form is completely allopatric and the associated workers and males are hardly separable by themselves from the typical *fuliginosus.*

Worker petiolar pilosity. In European series the longest erect hairs of the dorsal petiolar margin are consistently shorter than one-half the maximum width of the scape, whereas in Japanese series they are usually longer than one-half. Series from the following Asiatic localities were found however to be closer to the European type: Tokyo (MCZ); Ashoromura, Hokkaido

(Yasumatsu Coll.); Kongosan, Korea (Yasumatsu Coll.); Miao T'ai Tze, Shensi, China (W. L. Brown leg.; MCZ); Harbin, Manchuria (Yasumatsu Coll.); Okeanskaja, Siberia ("*capitatus*" syntypes).

Worker occipital outline. Series from northeastern Asia (Ashoromura, Kongosan, Miao T'ai Tze, Harbin, Okeanskaja) have unusually shallow occipital emarginations (viewed in perfect full face, the emargination 0.03 mm. deep or less). This condition occurred in only 7 out of 47 European nest series examined.

DISTRIBUTION. This species is widely distributed in the Palaearctic Region. It occurs in Ireland (O'Rourke, 1950), in England north to Lancashire and Yorkshire (Donisthorpe, 1927), in Norway north to Elverum and west to Søndeled and Lyngør (Holgersen, 1944), and in several localities in southern Sweden (Forsslund, 1947). I have determined specimens from Kuopio, southern Finland (O. Wellenius leg.; MCZ). Extensive collections studied during the course of the present work combine with the independent statements of many authors in a massive European literature to give the impression that *fuliginosus* is a common species throughout northern Europe. In the west it extends as far south as Centellas, Barcelona (de Xaxars leg.; MCZ), but has never been taken in North Africa, the Balearics, or the Canaries. In the east it is widespread in northern Italy and northwestern Yugoslavia (numerous series mostly in the MCZ) and extends through the mountains of central Yugoslavia (Zimmermann, 1934) to as far south as Mali Daiti and Tirana in Albania (Ravasini and Lona leg.; MCZ). I have seen a single series labelled "Syrien Libanon" (E. V. Bodemeyer leg.; Holgersen Coll.); the species is probably rare or local in this area since it was not in the substantial collection of the genus made by Dr. K. Christiansen in the mountains of Lebanon. Karawajew (1926) records it from the Krimea. It is apparently rare or absent in Central Asia (Menozzi, 1939; Eidmann, 1941). Bingham (1903) records it from Thana, near Bombay, but this is a rather incredible record, in the same class as a single specimen now in the MCZ labelled "Tutu River, North Borneo." Some records from eastern Asia have already been given in the section on geographic variation. Additional records accumulated during the present study include the following: Mt. Rokko and Yamashita, Hyogo Pref., Honshu (M. Azuma leg.; USNM); Mt.

Kajigamori, Shikoku (H. Okamoto leg. and Coll., MCZ); Kochi, Shikoku (Okamoto leg. and Coll.); central Korea, no further data (K. Yasumatsu Coll., MCZ).

ECOLOGY. Many European observers have reported independently on various aspects of the ecology of this ant, and together they present a reassuringly consistent picture. *Fuliginosus* nests primarily in standing tree trunks and rotting stumps, and only occasionally in and around the roots of trees, under stones, and in open soil. In a random field survey in Germany, Gösswald (1932) recorded 63 nests in wood, 2 under stones, and 5 in open soil. He found the species nesting most commonly in old poplars and willows in dry meadows. It is often locally abundant; O'Rourke (1950) notes that in Ireland it may become the dominant ant in oak woods.

Fuliginosus almost invariably constructs a carton nest. The composition of the carton has been analyzed by Stumper (1950), who finds that it consists primarily of macerated wood hardened with secretions from the mandibular glands. There may be some soil particles mixed in, especially in subterranean nests, but these constitute a very minor fraction. Stumper was unable to find supporting evidence for the old contention that several species of symbiotic fungi are normally grown in the carton walls.

Fuliginosus forages during both the day and night, forming long, conspicuous columns which usually lead to trees infested with aphids or coccids; the excreta of these latter insects forms a principal food source for the ant. In addition, many authors have observed workers carrying dead or crippled insects back to the nests.

Eidmann (1943) has studied overwintering in this species. A colony which he kept under observation through the autumn moved from a position in a tree bole to subterranean quarters directly beneath the tree. The winter carton nest had chambers twice the size of those in the summer nest, and its walls were conspicuously studded with grains of sand. Medium-sized and full grown larvae were found hibernating with the adults.

Winged reproductives have been taken in the nests from May to September. The nuptial flights apparently take place earlier than in other members of the genus; literature records span the period May 4 to July 27. The flights occur mostly in the afternoon, although some authors, such as Escherich and Ludwig

(1906), have suggested that they occur at night also. According to Donisthorpe (1927), the mating behavior shows early signs of parasitic degeneration. There is a marked decrease in the size difference between the two sexes, and the nuptial flight appears to have been partly suppressed. In one case Donisthorpe observed nestmates copulating on vegetation in the immediate vicinity of the parent nest.

Donisthorpe (1922) has also reviewed the extensive literature on colony founding in this species. It has been proven without any doubt to be a temporary social parasite on *Lasius umbratus* (= *mixtus*), which species was defined in the old sense and may well include *L. rabaudi* also. Numerous mixed colonies have been found in nature, and successful adoptions of dealate queens by host colonies have been repeatedly obtained under artificial conditions. This habit places *fuliginosus* in the extraordinary position of being a social hyperparasite, since *umbratus* is parasitic itself on members of the subgenus *Lasius*. In more recent years, Stärcke (1944) has obtained the experimental adoption of *fuliginosus* queens by colonies of *L. rabaudi* (= *meridionalis*), *L. niger*, and *L. alienus*.

SYNONYMY. *Lasius fuliginosus* var. *nipponensis* Forel. Lectotype by present selection, a worker in the Forel collection. Head and thorax partly crushed and not measurable. Pilosity of petiolar dorsal margin long, characteristic of the Japanese population already described.

Lasius fuliginosus var. *orientalis* Karawajew. Since the types are not available, synonymy in this case is tentative. The differences stated in the original description are of a trivial nature, and it would seem that if Karawajew had really had *spathepus* before him instead of *fuliginosus,* he would have noticed at least one of the several excellent characters which separate workers of these two species.

Acanthomyops fuliginosus capitatus Kuznetzov-Ugamskij. Lectotype by present selection, a worker in the MCZ labelled "Acanthomyops fuliginosus orientalis Karav. (=capitatus K.)/Far East. Station Okeanskaja, near Vladivostok." PW 0.78 mm. Possessing a shallow occipital emargination and short petiolar hairs, both of which characters seem to predominate in northeastern Asia. Kuznetzov-Ugamskij (1929a) later used Karawajew's name *orientalis* instead of *capitatus,* without disclosing his reasons for creating the synonymy. If trinomens are to be used at all for this population, it will first have to be ascertained whether the types of the two forms share the same pilosity and cephalic outline characters.

LASIUS CRISPUS Wilson, new species

(Subg. *Dendrolasius*)

DIAGNOSIS. An eastern Asian species most readily distinguished by the aberrant pilosity and pubescence of the queen caste.

Queen. (1) Body and appendage hairs much finer than in *fuliginosus,* many curved at the tip or even sinuate. On the appendages, where the pilosity is predominantly decumbent to subdecumbent, the hairs are frequently wicket-shaped in addition, recurving to touch the cuticular surface with their tips.

(2) Body pubescence very sparse or absent, so that the entire cuticular surface is moderately to strongly shining. The appendages are densely covered with appressed hair, the legs somewhat more so than the scapes.

(3) Viewed from the side the crest of the petiole thin and acute; the entire posterior margin of the petiole feebly concave in each of the three specimens examined.

(4) Viewed in full face the genal margins nearly straight, curving inward only near the mandibular insertions. As a result the occipital region appears proportionately wider, and the entire head more sagittate, than in *fuliginosus.*

(5) The median clypeal keel, which is feebly developed in *fuliginosus,* is completely lacking in *crispus.*

Worker. Two workers from Ueda, Honshu, and a small series from central Korea are tentatively and with great reservation placed in this species and used for the following diagnosis.

(1) The standing hairs of the second and third gastric tergites, anterior to the extreme posterior strips, as long as those of the pronotum or longer. In the Ueda series but not in the Korean series, femora with numerous outstanding decumbent to suberect hairs. Cephalic and gastric pilosity denser than in *fuliginosus.*

(2) Petiolar crest viewed from the side thinner and sharper than in *fuliginosus,* the anterior and posterior faces less convex (Pl. 2, Fig. 8).

Male. (1) In side view the anterior and posterior faces of the petiole taper equally to form a narrow, sharp crest. Otherwise very similar to *fuliginosus.*

(2) Terminal segments of maxillary palp highly variable in length as in other *Dendrolasius,* but showing no sign of ankylosis.

(3) Pygostyle and subgenital plate as in *fuliginosus.*

HOLOTYPE. An alate queen collected at Katsura-hama, Shikoku, on August 7, 1940 (H. Okamoto leg. and Coll.). HW 1.48 mm. An identical paratopotype queen is in the MCZ. These two specimens and the Kochi queen have a more extreme pilosity than the Ueda queen; virtually every hair shows curving to some degree, and many of the longer body hairs are sinuate.

FURTHER DESCRIPTION. *Queen.* HW of paratopotype 1.58 mm., of Ueda queen 1.55 mm., of Kochi City queen 1.52 mm.

Worker. PW of Ueda workers 0.64 and 0.72 mm., of Korean series 0.77-0.87 mm.

Male. HW of paratopotype male 1.08 mm., of Ueda series 1.04-1.26 mm. Genitalia identical to that of *fuliginosus.*

DISTRIBUTION. SHIKOKU: Katsura-hama, 2 winged queens and a male; Kochi, a winged queen, IX-5-1935 (H. Okamoto leg. and Coll.). HONSHU: Ueda, a winged queen and 11 males, VI-1934; 2 workers, VI-6-1936 (S. Miyamoto leg.; Yasumatsu Coll. and MCZ). KOREA: ''central Korea'', many workers (Yasumatsu Coll. and MCZ).

Lasius buccatus Stärcke

(Subg. *Dendrolasius*)

Lasius buccatus **Stärcke, 1942, Tijdschr. Ent., 85: 27–28, figs. 6, 7; queen, male; original description. Type locality: Dragocaj-Sarajevo, Bosnia.**

DIAGNOSIS. I have not been able to examine the types, but from Stärcke's figures and description this appears to me to be a good species separated from *fuliginosus* by several cephalic characters in the queen and male.

Queen. (1) A sharp median carina runs from the junction of the clypeus and the frontal triangle to a small shallow pit in the center of the clypeus. The *fuliginosus* clypeus invariably has an indistinct, obtuse median keel running most of its length, but I have never seen the posterior segment prominently developed. This keel in *fuliginosus* often dips slightly in the middle, and in one series, from Imer, Venezia Tridentina (MCZ), the dip is even developed into a shallow, very indistinct depression, which nonetheless still does not approach the condition figured by Stärcke for *buccatus.*

(2) The head of *buccatus* is narrower than in *fuliginosus,* according to Stärcke about 1.03 × longer than broad (HL/HW). In none of the *fuliginosus* series I have measured does the HL exceed 0.95 × the HW.

(3) Head narrower than the thorax. No specific measurements are given by Stärcke, but if true, this character represents an extraordinary exception to the rule for *Dendrolasius.*

(4) The antenna dark brown, nearly the same color as the head. *Fuliginosus* has medium brown antennae which contrast against the blackish brown head.

Male. (1) Lateral margins of the head, especially the genal margins, more convex than in *fuliginosus.* From Stärcke's figure, the head width just below the eyes is nearly the same as that above the eyes; in *fuliginosus* it is only about 0.9 × as great. As a result the *buccatus* head presents an almost circular outline in frontal view.

(2) Mandibles with seven well developed teeth including the apical. In the single male the dental pattern is the same on both mandibles: the fifth tooth and seventh tooth (the latter on the basal angle) are reduced in size. In *fuliginosus* adventitious denticles are often developed at random along the masticatory border but they are never as large and seldom as numerous as the teeth depicted by Stärcke for *buccatus*, and they never form a constant pattern.

LASIUS TERANISHII Wheeler

(Subg. *Dendrolasius*)

Lasius teranishii Wheeler, 1928, Boll. Lab. Zool. Portici, **21:** 120; queen; *nom. pro Lasius umbratus,* Teranishi, 1927 [*nec* Nylander]. Type locality: Nokkeuchi, Hokkaido.

Lasius umbratus, Teranishi, 1927, Zool. Mag., **39:** 90, 92–93, figs. 6, 6A. Reprinted in ''Works of Cho Teranishi, Memorial Volume,'' 1940, pp. 51, 53–54. [*nec* Nylander.]

Lasius ouchii Teranishi, 1940, ''Works of Cho Teranishi, Memorial Volume,'' posthumously published section, p. 76; queen. NEW SYNONYMY (objective synonym of *L. teranishii* Wheeler).

DIAGNOSIS. It is clear from Teranishii's figures that the holotype and single known specimen of this species is not a *Chthonolasius,* as previously considered, but a *Dendrolasius* intermediate in habitus between the "alpha" — form queen of *fuliginosus* and the extreme "beta" — form queen of *spathepus.* Its membership in this subgenus is suggested by the prominent anterior curve of the scutum overhanging the pronotum, by the thickened profile of the petiolar scale, by the more cordate head shape, and by the blackish brown body coloration. It resembles *spathepus* in possessing conspicuously flattened scapes, femora, tibiae, and metatarsi, and in lacking standing hairs on the body. It differs markedly from that species in having an "alpha" head shape, closely resembling that of *fuliginosus.* Also, Teranishi makes no mention of the presence of any aberrant appendage pilosity of the type found in *spathepus.* The petiolar scale is symmetrical in profile, with an evenly rounded dorsal crest, a condition shared with *fuliginosus.*

LASIUS SPATHEPUS Wheeler
(Subg. *Dendrolasius*)

Lasius spathepus Wheeler, 1910, Biol. Bull., **19**: 130–131, fig.; queen; original description. Type locality: none specified, by inference Nishigahara, near Tokyo.
Lasius fuliginosus var. *spathepus,* Teranishi, 1927, Zool. Mag., **39**: 50.
Lasius spathepus, Wheeler, 1928, Boll. Lab. Zool. Portici, **21**: 121.

DIAGNOSIS. A Japanese and Korean species marked by several excellent characters in all three castes but best distinguished by the aberrant, "beta"-form queen.

Worker. (1) Head broader, occiput usually less concave, and scapes shorter relative to head width than in other *Dendrolasius.*

(2) Antennal scapes flattened to the extent that for most of their length the minimum measurable width at any point is less than half the maximum measurable width at the same point. Tibiae and metatarsi also noticeably flattened.

(3) Hairs of scapes and legs sparser and longer than in other *Dendrolasius.* The standing hairs seen in relief when the hind

tibia is viewed in the plane of its minimum width are often half as long as the greatest width measurement obtained along the length of the tibia in this view, or longer. Tibial hairs appressed to suberect, the majority tending to decumbent.

(4) The petiole seen in frontal view subrectangular; the dorsal border always emarginate to some degree. In side view the anterior face curving back abruptly just above the level of the spiracle, in contrast to the posterior face, which is gently and evenly convex from the posterior foramen to the crest (Pl. 2, Fig. 6).

(5) Propodeum viewed from the side typically higher and more prominent relative to the thorax than in other *Dendrolasius.* A single series from Nanzan, Korea, represents an extreme deviant from this character and is well within the range of variation of *fuliginosus.*

Queen. (1) Averaging and ranging larger than other *Dendrolasius;* HW 1.96-2.03 mm.

(2) Head much broader than long, with a deeply emarginate occipital border and strongly convex sides which curve in sharply at the mandibular insertions. The mandibles exceptionally small relative to the head.

(3) Scapes, femora, tibiae, and metatarsi greatly flattened, the minimum width of the scape at midpoint about half the maximum width.

(4) The broad surfaces of the scape coarsely and evenly punctate.

(5) The dorsal border of the petiole emarginate for nearly its entire extent. In side view the scale is anteriorly truncated as in the worker.

(6) The scapes, tibiae, and metatarsi densely covered with long, predominantly suberect, coarse, silvery yellow hairs. On the tibiae and metatarsi these form two layers, those in the lower, short and densely packed and those in the upper, long, curved and sparse.

(7) Ground pubescence completely lacking on the body. Hairs are limited mostly to the mandibles, clypeus, gula, posterior third of the head, petiole, anterior first gastric tergital surface and posterior gastric tergital margins. The alitrunk is completely lacking in pilosity of any kind except for a few scattered short hairs on the propodeum.

(8) The body is very feebly sculptured and strongly shining, except for the petiole and anterior clypeal margin, which are shagreened; and the mandibles, which are longitudinally striate.

(9) Median clypeal carina well developed posteriorly but vanishing in the planed, shagreened anterior fourth of the clypeus.

Male. (1) Averaging and ranging larger than other *Dendrolasius;* HW 1.13-1.27 mm.

(2) Scapes and tibiae distinctly flattened.

(3) Petiole in frontal view distinctly emarginate and much broader than in other *Dendrolasius.* Petiolar outline in side view similar to that described for the worker.

(4) Pygostyle as in *Chthonolasius,* i.e. thicker than in *Lasius s. s.* and tapering gradually from base to tip (Pl. 2, Fig. 12). The subgenital plate distinctive in shape: the posterior margins between the setiferous lobes and posterior angles more deeply convex than in *fuliginosus* and *crispus,* causing the setiferous lobes to project back more prominently (Pl. 2, Fig. 10).

(5) Scape and tibial pilosity longer and sparser than in other *Dendrolasius.*

HOLOTYPE. A queen in the MCZ labelled ''Japan. Kuwana Coll. 1910.'' HW 2.03 mm.

DISTRIBUTION. Following are all of the records verified during the present study. HONSHU: Kanagawa Pref. (H. Sauter leg.; MCZ); Kamakura, Kanagawa Pref. (F. Silvestri leg.; MCZ); Odawara, Kanagawa Pref., winged queens and males VI-22-1952 (M. Kubota leg.; MCZ); Yokohama (L. Gressitt leg.; MCZ); Tokyo (Gressitt leg.; MCZ); Ueda (S. Miyamoto leg.; Yasumatsu Coll.); Hiroshima (Miyamoto leg.; Yasumatsu Coll.). SHIKOKU: Mt. Kajigamori (H. Okamoto leg. and Coll.). KYUSHU: Kubotayama (Yasumatsu Coll.); Hikosan (Yasumatsu leg. and Coll.); Sobosan (Fujino and Yasumatsu leg.; Yasumatsu Coll.); Magari-fuchi (Hori and Fujino leg.; Yasumatsu Coll.); Fukuoka (Shirozu leg.; Yasumatsu Coll.). KOREA: Seoul (Yasumatsu Coll. and MCZ); Mt. Kangaku, near Seoul (K. S. Ryu leg.; Yasumatsu Coll.); ''Nanzan'' (Shirozu leg.; Yasumatsu Coll.); Mt. Kongo (Shirozu leg.; Yasumatsu Coll.).

SYNONYMY. Wheeler (1928) was wrong in considering Forel's *L. fuliginosus* var. *nipponensis* a synonym of *spathepus.*

The *spathepus* queen does not represent, as he supposed, the "beta" form of a *fuliginosus*-like species. Rather *spathepus* and *fuliginosus* occur together in Japan as distinct species and are separated by excellent characters in all three castes.

[LASIUS NEMORIVAGUS Wheeler]

(Subg. *Chthonolasius*?)

Lasius nemorivagus **Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, 55:** 123; queen; original description (Baltic amber).

DIAGNOSIS. *Queen.* According to Wheeler, maxillary palps typical for the subgenus *Lasius,* but head broader than thorax, a *Chthonolasius* and *Dendrolasius* character. Funicular joints II-VI broader than long, VII-X as broad as long. Body more thickset, appendages stouter than in *schiefferdeckeri.* Size small, total length 6 mm., the lower limit later given by Wheeler (1917a) for the queen caste of "*neoniger*" (*sitkaensis, niger,* and *neoniger*). Body with sparse erect hairs; appendages presumably bare.

HOLOTYPE. The single type specimen was probably lost with the rest of the Königsberg Geological Institute Collection during the Second World War.

LASIUS UMBRATUS (Nylander)

(Subg. *Chthonolasius*)

Formica umbrata **Nylander, 1846, Acta. Soc. Sci. Fenn., 2: 1048–1050; queen, male; original description. Type locality: Helsinki, by selection of Stärcke (ref. below).**

Formica mixta **Nylander, 1846, *ibid.,* pp. 1050–1052; queen; original description. Type locality: Upsala. NEW SYNONYMY.**

Lasius umbratus mixtus, **Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 47.**

Formica affinis **Schenck, 1852, Jahrb. Ver. Nat. Nassau, 8: 62–63; worker, queen, male; original description. Type locality: Weilburg, Nassau, Germany, by present selection. NEW SYNONYMY.**

Lasius umbratus affinis, **Forel, 1874, *loc. cit.***

Formica aphidicola **Walsh, 1862, Proc. Ent. Soc. Phila., 1: 310; worker, male; original description. Type locality: Rock Island, Illinois, by virtual designation. NEW SYNONYMY.**

Lasius umbratus mixtus var. *aphidicola,* Emery, 1893, Zool. Jahrb. Syst., **7:** 640.

Lasius umbratus aphidicola, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 425.

Lasius umbratus var. *mixto-umbratus* Forel, 1874, *op. cit.,* p. 48; worker; original description. Type locality: by inference, Switzerland. NEW SYNONYMY.

Lasius umbratus var. *exacutus* Ruzsky, 1904, Kasan Univ. Obschchestvo estestvoispytatelei Protokoly Zasiedanii, no. 206, p. 15; worker; original description (in Russian). Type locality: Caucasus, 8000 feet. NEW SYNONYMY.

Lasius umbratus var. *mixto-affinis* Ruzsky, 1904, *loc. cit. Nomen nudum.*

Lasius umbratus var. *mixto-bicornis* Ruzsky, 1905, "Formicariae Imperii Rossici," Schrift. Naturforsch.-Ges. Univ. Kasan, **38:** 292. *Nomen nudum.*

Lasius umbratus var. *affino-umbratus* Donisthorpe, 1914, Ent. Rec., **26:** 40; worker; original description. Type locality: Tenby, England. NEW SYNONYMY.

Lasius umbratus var. *przewalskii* Ruzsky, 1915, Ann. Mus. Zool. Acad. Sci. Petrograd (Academii Nauk S. S. S. R., Leningrad, Zoologischeskii muzei), **20:** 434; worker; original description (in Russian). Type locality: Valley of River Tetunga, northeastern Tibet. NEW SYNONYMY.

Lasius umbratus exacutus var. *prczewalski* [!], Emery, 1924, Gen. Insect. (Wytsman), Fasc. **183:** p. 234.

Lasius bicornis exacuta var. *prezcwalskii* [!], Menozzi, 1939, Atti Soc. Ital. Sci. Nat., **78:** 32.

Formicina umbrata distinguenda Emery, 1916, Rend. Acc. Bologna, pp. 64–65; worker, queen; original description. Type locality: Bologna. NEW SYNONYMY.

Formicina umbrata var. *hybrida* Emery, 1916, *ibid.,* p. 66. Synonymy by Stärcke, 1937, Tijdschr. Ent., **80:** 57.

Formicina umbrata var. *nuda* Bondroit, 1917, Bull. Soc. Ent. Fr., **86:** 176. Synonymy by Stärcke, *op. cit.,* p. 56.

Formicina umbrata var. *sabularum* Bondroit, 1918, *op. cit.,* **87:** 31. Synonymy by Stärcke, *op. cit.,* p. 56.

Formicina belgarum Bondroit, 1918, *op. cit.,* **87:** 31; worker, queen; original description. Type locality: none designated. NEW SYNONYMY.

Lasius umbratus var. *belgarum,* Stärcke, 1937, *op. cit.,* **80:** 57.

Lasius bicornis var. *citrina* Emery, 1922, Bull. Soc. Ent. Ital., **54:** 12; worker; original description. Type locality: Monte Gargano, Puglia, Italy, by present restriction. NEW SYNONYMY.

Lasius umbratus var. *viehmeyeri* Emery, 1922, *ibid.,* pp. 13–15, fig. 2;

worker, queen; original description. Type locality: Erymanthos, Peloponnesus, Greece. NEW SYNONYMY.

Lasius viehmeyeri, Stärcke, 1937, *op. cit.*, **80**: 53.

Lasius silvestrii Wheeler, 1928, Boll. Lab. Zool. Portici, **20**: 120–121; queen; original description. Type locality: Mt. Maya, nr. Kobe, Honshu. NEW SYNONYMY.

Lasius viehmeyeri var. *dalmatica* Stärcke, 1937, Tijdschr. Ent., **80**: 53–54; queen; original description. Type locality: Knin, near Zara, Yugoslavia. NEW SYNONYMY.

Lasius umbratus var. *hirtiscapus* Stärcke, 1937, *ibid.*, p. 43; queen; original description. Type locality: ''Kiczera,'' Beskids, Czechoslovakia. NEW SYNONYMY.

Lasius umbratus distinguendus var. *cereomicans* Stärcke, 1937, *ibid.*, pp. 48–49; worker, queen, male; original description. Type locality: Aosta, Piemonte, Italy. NEW SYNONYMY.

Lasius silvestri [!] var. *osakana* Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18**: 278; queen; original description. Type locality: Ikeda, Osaka Pref., Honshu. NEW SYNONYMY.

Chtonolasius [!] *affinis* var. *nyárádi* Röszler, 1943; Zool. Anz., **144**: 47–48; worker, queen; original description. Type locality: Nyárádtö, Rumania. NEW SYNONYMY.

Lasius umbratus epinotalis Buren, 1944, Iowa State Coll. Jour. Sci., **18**: 297–298; worker; original description. Type locality: Bellevue, Iowa. NEW SYNONYMY.

Lasius subumbratus epinotalis, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 424.

DIAGNOSIS. *Queen.* (1) Most of the body surface covered with abundant, relatively short, silvery yellow, predominantly erect hairs. The hairs on the first three gastric tergites with maximum length variable internidally, 0.05-0.11 mm., never more than one-half the maximum width of the hind tibiae at midlength, and often less than one-third; very variable in density, never less than 20 hairs visible above the dorsal profile of the first gastric segment seen in perfect side view and usually more than 30, but never dense enough to overlap one another extensively. Erect hairs forming a fringe on the dorsal crest of the petiole, their maximum length close to that of the gastric hairs. The longest hairs of the alitrunk are on the scutellum, maximum length 0.12-0.21 mm. Maximum length of scutal hairs 0.05-0.15 mm. (see also under geographic variation). Maximum length of cephalic hairs exclusive of those on the clypeus 0.09-

0.11 mm. Body hairs mostly straight or feebly curved, rarely strongly curved (on propodeum) and never sinuate. Standing hairs may or may not be present on the appendages (see also under geographic variation). All of body and appendages densely covered with short, whitish pubescence which is completely appressed on the body and appressed to decumbent on the appendages; on the gaster it is often abundant enough to obscure partly the shining cuticular surface and to present a whitish overcast to the naked eye.

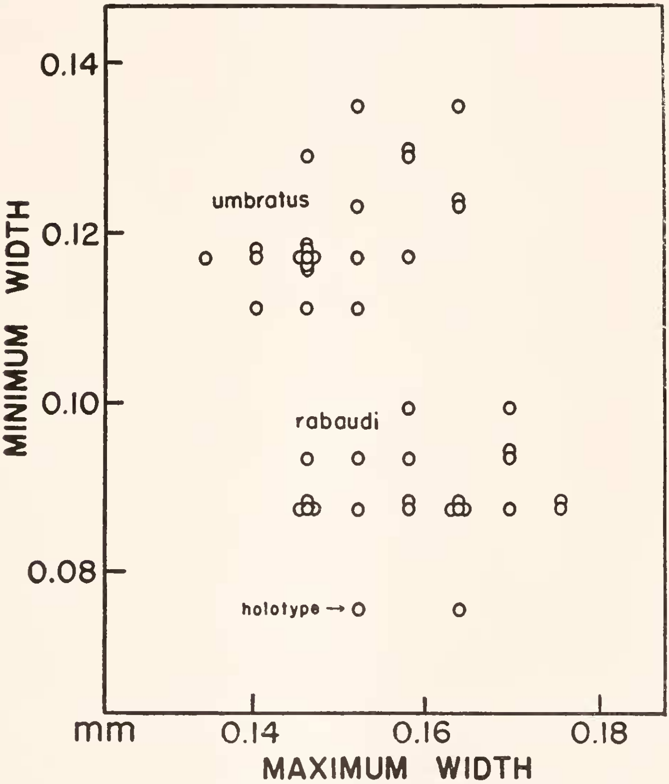

Fig. 15. Flattening of the scape in the queen caste of the two Palaearctic sibling species *L. umbratus* and *L. rabaudi.* This is the principal character separating the two species. Further explanation in the text. Nest series chosen at random; no more than two queens per series were measured.

(2) HW ranging 1.40-1.82 mm. in 45 nest series measured (see also under geographic variation). SI of size extremes 75 and 81.

(3) Petiole in frontal view tapering gradually but distinctly from the level of maximum width (just above the foramina) to the dorsal crest, the width just ventral to the dorsolateral angles 0.9 × the maximum width or less but the frontal outline rarely subquadrate as in *rabaudi.* Dorsal crest extremely variable in shape, from very feebly concave or even straight to deeply concave with the emargination almost right-angular. The dorsolateral angles always broadly rounded. In side view the scale is narrow and with an acute dorsal crest.

(4) The scape short-elliptical to circular in cross-section, never conspicuously flattened, the minimum width at the midpoint 0.11 mm. or greater (Fig. 15). The third funicular segment 1.0-1.5 × longer than broad.

(5) Body medium to dark brown, the appendages lighter, light to medium brown.

Worker. (1) Pilosity and pubescence as in queen. Maximum length of hairs of first gastric tergite anterior to the extreme posterior strip 0.06-0.08 mm., not exceeding one-half the maximum width of the hind tibia at midlength. Alitruncal and cephalic hairs with maximum length of about 0.11 mm.

(2) Petiole in frontal view tapering slightly from the widest point, just above the foramina, to the dorsal crest. The dorsal crest broad and very variable in outline, from flat or even feebly convex to deeply concave; the emargination rounded or angular, never as deep as in *bicornis,* i.e. the width (taken at the midpoint of the depth measurement) always exceeds the depth. Intranidal variation considerable; the petiole in a single series may range from flat to distinctly emarginate. In side view the scale is relatively narrow, its dorsal crest acute.

Male. (1) Pilosity and pubescence essentially the same as in the queen and worker, except that hairs of the first three gastric tergites are more frequently subdecumbent-suberect. Despite this greater tendency toward obliqueness, the hairs of the first gastric tergite are still too sparse to show much overlap, and their maximum length (excluding those on the extreme posterior strips) ranges internidally 0.07-0.08 mm., or always less than 0.7 × the maximum width of the hind tibia at its midlength.

Maximum length of scutellar and cephalic hairs (excluding those on the clypeus) 0.09 mm.

(2) HW 0.85-1.23 mm. in 15 nest series measured; SI of the extremes 62 and 66.

(3) Petiole in frontal view tapering dorsally as in queen and worker. Dorsal margin flat to deeply emarginate, the emargination rounded or angular, never greater than semicircular or right-angular. The scale in side view relatively thin, with an acute dorsal crest.

LECTOTYPE. A dealate queen in the Helsinki Museum, selection by Stärcke (1937). From Stärcke's description it is clear that this specimen is large (head width across and including eyes 1.71 mm.) and at one extreme of the normal allometric variation in head shape, pilosity, etc. (see section below).

GEOGRAPHIC VARIATION. *Size and correlated allometric characters in the queen.* Allometric variation in several diverse characters is quite extensive and complicated in the European population of *umbratus*. This has been the principal origin of the ponderous and almost hopelessly confusing mass of synonymous specific, subspecific and varietal names that have been piled around *umbratus* in past years. The single most important synonym of *umbratus* is the "species" *mixtus* which, as will be shown below, rests at one extreme of allometric variation opposite the "typical" *umbratus*. When *mixtus* falls into synonymy, most of the other satellite forms of *umbratus* fall with it, since these have been erected on the kind of characters which are supposed to be of species value in distinguishing *mixtus*.

According to Stärcke (1937), the *mixtus* holotype differs from the *umbratus* lectotype in the following characters: (1) small size (HW across and including eyes 1.50 mm.), (2) occipital border less concave, (3) pubescence denser, (4) puncturation of the head finer, so that at a magnification of 70× the interstices are at least twice as wide as the punctures themselves (in the *umbratus* lectotype the cephalic sculpture consists of saucer-shaped depressions much wider than the interstices), (5) tibiae bare of pilosity, head with sparse pilosity (erect hairs abundant on tibiae of *umbratus* lectotype), (6) penultimate funicular segment (no. 10) broader than long (longer than broad in the *umbratus* lectotype). To these queen characters we can add the one often advanced as diagnostic for the worker caste: standing hairs present on the scape and tibiae in *umbratus,* absent in *mixtus.* According to Stärcke, *mixtus* workers are characterized by an absence of pilosity in the center of the head, combined with a sinuate to flat dorsal petiolar crest; *umbratus* has "appreciable" pilosity in the center of the head, combined with a more deeply emarginate dorsal petiolar crest. Stärcke abandons

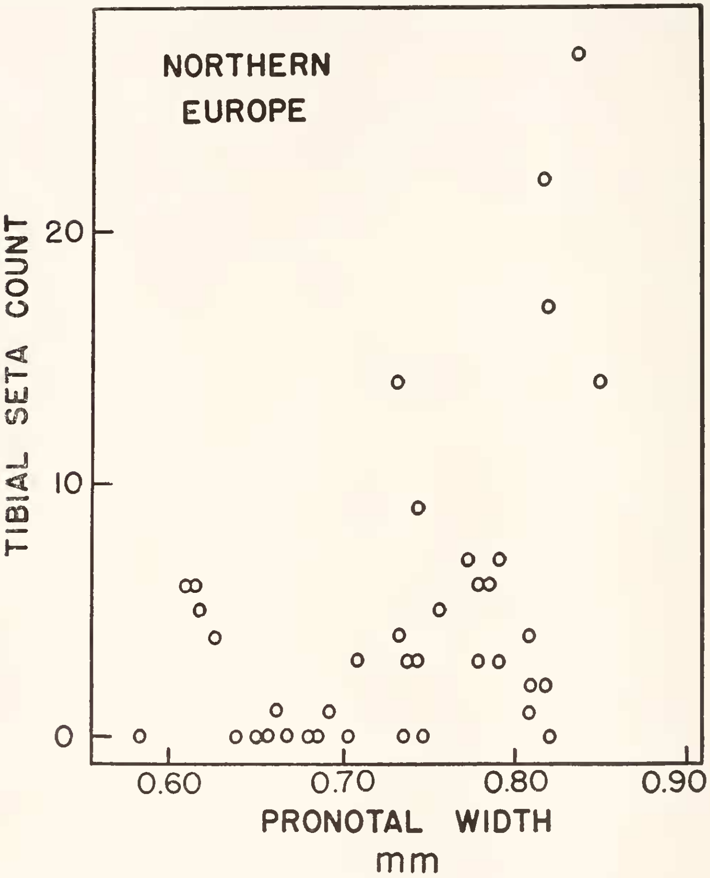

Fig. 16. Pronotal width-tibial seta count relationship in a random northern European sample of *L. umbratus* workers. Nest series chosen at random; no more than two workers per series were measured.

the appendage pilosity character, since he considers that a southern race of *umbratus* (*distinguendus* Emery) lacks the diagnostic standing hairs and must be separated in other ways.

During the present study I have been fortunate in being able to study large numbers of series of *umbratus* from all over Europe and North Africa, including peripheral areas in Spain, Algeria, Lebanon, European Russia, Finland, Scandinavia, and England. Over 40 of the series contained queens. As a result I now feel reasonably confident in saying that each of the characters listed above for both female castes grades through evenly from the "*umbratus*" extreme to the "*mixtus*" extreme and that no single character, or combination of characters, can be used to separate *umbratus* and *mixtus* as species.

Furthermore, all of these characters except pubescence show some degree of correlation with total body size and with each other. In other words, they appear to be simply pleiotropic expressions of a single strong allometric trend. Specifically, as size increases, the occipital concavity deepens, the cephalic punctures broaden and the body surface grows more opaque, the standing hairs on the body and appendages grow proportionately denser, and the funicular segments elongate. Pubescence alone varies erratically and independently of the other characters.

The amount of size variation and the degree of expression of the pilosity character (its regression slope), are in turn subject to geographic variation. In general, queens from southern areas (Spain, Italy, Yugoslavia, Lebanon) are less size variable and fail to develop standing tibial pilosity with increase in size. The maximum HW range ascertained for the southern population as a unit was 1.64-1.82 mm., while that of the northern population was 1.49-1.80 mm. In both cases there is an unexpected skewness toward the smaller size classes. The northern queens begin to develop standing hairs on the scapes and tibiae above a HW of about 1.60 mm., and the largest individuals have dense standing pilosity on the scape (Stärcke's var. *hirtiscapus*). Thus, the northern population shows extensive variation, from the smallest "*mixtus*" individuals up to the largest, hairy forms. The southern population, on the other hand, exhibits only the upper half of the size variation shown by the northern population, thereby missing the "*mixtus*" form, and in addition the largest individuals do not develop standing hairs on the scapes as do northern queens of comparable size.

There are therefore only two real detectable differences between the extreme northern and southern European samples: (1) the southern sample apparently lacks the lower segment of the size range exhibited by the northern sample; (2) queens above 1.60 mm. develop standing hairs in the northern but not in the southern sample. Contrary to Stärcke's statement, I have been unable to find any difference between the northern and southern populations in the length of scutal and cephalic hairs.

Numerous North American series examined ranged in HW from 1.40 to 1.58 mm., averaging significantly smaller than all of the Palaearctic samples. As might be expected, they conform to the *"mixtus"* type in the allometric characters just described.

Geographic variation of queen appendage pilosity is apparently reflected in the worker caste, since the *"umbratus"* character is rare or absent in workers from the Mediterranean perimeter. When pilosity in northern series is plotted against size, a simple allometric regression zone is obtained (Fig. 16). As in the queen, there is no evidence of a breakdown into two or more species. Much the same relationship apparently holds for cephalic pilosity, one of the two characters mentioned by Stärcke. Stärcke's second worker character, petiole shape, grades through from one extreme (straight dorsal border) to the other (deeply concave border), as already stated in the diagnosis. It does not show any geographic trend.

Asiatic queens. Umbratus is evidently less common in eastern Asia than in Europe and North America, being outnumbered in collections from there by *L. rabaudi.* I have seen only seven queens in the course of this study, including the holotypes of *silvestrii* Wheeler and *osakana* Santschi, and specimens from Nishiashoromura, Hokkaido (Matsuda leg.; Yasumatsu Coll.), Tokyo (L. Gressitt leg.; MCZ), Ryūjin, Wakayama Pref., Honshu (M. Azuma leg.; MCZ), and Sian Air Field, Shensi, China (W. L. Brown leg., MCZ). These are consistently large, HW ranging between 1.68 and 1.84 mm., and have somewhat more quadrate heads than European queens of comparable size, i.e. the heads taper less strongly anterior to the eyes. The *silvestrii* holotype and Ryūjin queen have an unusual pilosity feature: the hairs on the scapes and legs are very dense and relatively short;

those on the legs are predominantly subdecumbent, while those on the scapes are subdecumbent-suberect. The *osakana* holotype and Tokyo queens are not distinguishable from large northern European *umbratus* in pilosity, and hardly distinguishable in head shape. The Hokkaido and Shensi specimens are conveniently intermediate in pilosity between the *silvestrii* holotype and northern European *umbratus* and within range of variability of the latter in head shape. In general, the eastern Asiatic material is the most divergent of any single geographic sample, but the meager evidence available weighs against according it even conventional subspecific rank.

Lebanese queens. Two alate queens from the mountain above the Kammouha Plain (K. Christiansen leg.; MCZ) are peculiar in that the petiolar scale seen from the side is abruptly narrowed at midlength, so that the upper half is conspicuously thinner than the lower. In frontal view the dorsal margin is deeply and angularly emarginate. Both features represent extremes in what is normally a very variable structure in the European population. In other ways the queens are typical *umbratus.*

Worker eye size. The North American population as a unit has proportionately larger eyes, i.e. a higher EW-HW regression zone, than the European population as a unit, but there is still a great deal of overlap between the two (Fig. 17).

DISTRIBUTION. *Umbratus* is widespread over both Eurasia and North America. Our present knowledge of its distribution in Eurasia is unfortunately limited due to its past erroneous identification with the cryptic species *rabaudi* and the present dearth of diagnostic characters in the worker. I have listed below those records which I have verified myself through examination of the queen caste.

ENGLAND: "Wand" (MCZ). NORWAY: Asker, Oslo (H. Holgersen leg. and Coll.); Roa, Opland (Holgersen leg. and Coll.). SWEDEN: Ludgo, Södermanland (K.-H. Forsslund Coll.); Ekerö, near Stockholm (Forsslund leg. and Coll.); Österåker, Stockholm (Forsslund leg. and Coll.); Enköpling, Uppsala (Forsslund leg. and Coll.); Grangärde, Kapparberg (Forsslund leg. and Coll.). FINLAND: Helsinki (O. Wellenius leg.; USNM). NETHERLANDS: Den Dolder (A. Stärcke leg.; Forsslund Coll.); Roermond (J. K. A. van Boven leg.; MCZ). GERMANY: Tharandt, near Dresden (W. M. Wheeler leg.;

MCZ). SWITZERLAND: Roveredo (H. Kutter leg. and Coll.); Flawil (Kutter leg. and Coll.); Bruggen (Kutter leg. and Coll.); Saint Aubin (Kutter leg. and Coll.); Morges (A. Forel leg.; MCZ); Lausanne (M. Bibikoff leg. and Coll.). AUSTRIA: Plöcken Region (C. Mader leg.; Holgersen Coll.). CZECHOSLOVAKIA: Kroměříž (O. Fiala leg.; MCZ). HUNGARY: Nagytétény (P. Röszler leg.; MCZ). ITALY: San Nassaro, Lombardy (Kutter leg. and Coll.); Valbrona, Lombardy (B. Finzi leg.; MCZ); Monte Vederne, Venezia Tridentina (B. Finzi leg.; MCZ); Trieste (Finzi leg.; MCZ); Roiano, near Trieste (Finzi leg.; MCZ). YUGOSLAVIA: Parenzo and Momiamo, Istrian Peninsula (Finzi leg.; MCZ); "Podcetrtek" (Jaeger leg.; MCZ); eastern Bosnia (Milch leg.; MCZ). ALBANIA: Tomorica (Ravasini and Lona leg.; MCZ). LEBANON: Mt. above Kammouha Plain, 1500 meters, 2 alate queens (K. Christiansen leg.; MCZ).

The several verified Asiatic records have been discussed in the section on geographic variation. There are a great many literature records from Eurasia available, but these are of course rendered useless in the absence of their recognition of *L. rabaudi*. Several might be mentioned, however, in order to obtain a more complete picture of the range of the "*umbratus* group" in Eurasia: Daghestan (Kuznetzov-Ugamskij, 1929b); Dairen (Eidmann, 1929); Tatsienlu, Sikang (Eidmann, 1941); Nikolsk-Ussurijsk, Soviet Maritime Territory (Kuznetzov-Ugamskij, 1929a). In addition, I have seen indeterminate workers belonging to the group from Genzan, Korea (S. Kumashiro leg.; Yasumatsu Coll.) and Harbin, Manchuria (Y. Mori leg.; Yasumatsu Coll.).

In eastern North America *umbratus* occurs from Nova Scotia south to the Gulf States. I have verified the following records from southeastern Canada. NOVA SCOTIA: Bridgewater, a dealate queen (MCZ). NEW BRUNSWICK: Shediac Cape (Hubbard leg.; MCZ). QUEBEC: Kingsmere (MCZ); Hull (W. M. Wheeler leg.; MCZ). ONTARIO: Toronto (MCZ); Ottawa (MCZ); Plantagenet (E. O. Wilson leg.; MCZ); Point Pelee and Pelee Island (M. Talbot leg. and Coll.). *Umbratus* is generally abundant from New England south to the southern Appalachians of North Carolina and Tennessee. It is rare in the Gulf States, being known only from the following several records. GEORGIA: Blood Mountain, Union Co. (H. T. Vanderford leg.; USNM). FLORIDA: "Camp Torreya", Liberty Co. (H. K. Wallace leg.; UMMZ, MCZ). ALABAMA: Decatur, Morgan Co. (Wilson leg.; MCZ); Fayette, Fayette Co. (B. D. Valentine leg.; MCZ); Tuscaloosa (Wilson leg.; MCZ); Pollard, Escambia Co. (Wilson leg.; MCZ). MISSISSIPPI: Boyle, Bolivar Co. (M. R. Smith leg.; MCZ).

Westward, *umbratus* is abundant through North Dakota, as evidenced by the large numbers of collections made in many localities in that state by G. C. Wheeler and his students. It appears to be relatively common in the southern Rockies, but sparse to absent over most of the rest of western North America. There is a good possibility that its distribution west of the Great Plains is influenced in large part by competition from related species. It has never been taken within the range of *L. vestitus*, i.e. from northern California to British Columbia and northern Idaho. Moreover, in the mountainous areas where its range overlaps that of *L. subumbratus*, it tends to occur at lower elevations than that species and, so far as I know, the two have never been taken in the same immediate locality.

Following are the records from west of North Dakota accumulated during the present study. MONTANA: "Beaver Creek", 6300 feet (S. J. Hunter leg.; MCZ). IDAHO: Twin Falls (A. C. Cole leg. and Coll.). COLORADO: "Beaver Ranch" (W. M. Wheeler leg.; MCZ). UTAH: Kigalie Ranger Station, La Sal National Forest (C. T. Brues leg.; MCZ). ARIZONA: Williams, 7000 feet (Wheeler leg.; MCZ). NEW MEXICO: Ute Park, Colfax Co., 7400 and 7450 feet (2 series, A. C. Cole leg. and Coll., MCZ); Cimarron Canyon, 15 miles north of Cimarron, Colfax Co., 7100 and 7450 feet (2 series, Cole leg. and Coll.); Raton, Colfax Co. (C. T. Brues leg.; MCZ); Sapello Canyon, Beulah area, San Miguel Co., 7000 feet (Cole leg. and Coll., MCZ); Sandia Mountains, Bernalillo Co., 7700 feet (Cole leg. and Coll., MCZ); Mogollon Mountains, Catron Co., 8600 feet (Cole leg. and Coll., MCZ).

ECOLOGY. In the face of the revelation that *umbratus* has a common and hitherto poorly known Palaearctic sibling, *rabaudi* (Bondroit) (=*meridionalis* Bondroit), the great mass of European literature pertaining to this species and its many synonyms cannot be accepted without major qualifications. It is in fact very probable that much of the literature deals with *rabaudi* instead of *umbratus*. Among the European authors, only Stärcke (1937) seems to have fully realized the status and common occurrence of *rabaudi* and taken this taxonomic information into account in his ecological work. We are still very much in the dark as to whether the two species differ ecologically to any appreciable extent. In the following brief resumé, reference to European literature on *umbratus* is made with the understanding that both species may be included.

In Europe, according to Gösswald (1932), Zimmermann (1934), Donisthorpe (1927), and others, *umbratus* is less common than the prominent members of *Lasius s. s.* It prefers dry areas and rarely nests in moist soil; Skwarra (1929) found it very rare on the wet Zehlau moors of East Prussia. It usually nests under rocks, but also occurs in rotting wood (including the timbers of houses), at the foot of trees, or in open ground. On occasion it builds mounds. Its preferred habitat is woodland, but it has also been taken along forest borders and in cultivated fields. In North America, where no sibling comparable to *rabaudi* is yet known, *umbratus* differs from the European population in that it prefers moist soil, but it still shows the same latitude in specific nesting sites. The majority of colonies have been taken under stones, while the rest have been taken in or about rotting logs and stumps. I do not know of any case of this ant building mounds or even nesting in the open soil in North America, as it (or *rabaudi*) has been known to do in Europe. In the northern U. S. east of the Mississippi River, *umbratus* is limited mostly to moist woodland, where it occurs under a wide variety of conditions of soil texture and insolation. In Alabama and Florida, at the southern extremity of the range, all of the several colonies recorded were found in rotting logs and stumps in swampland. In the western U.S., all of the collections with ecological data that I have examined were made under rocks in open forest and along or near forest borders. In New Mexico, A. C. Cole took this species between 7100 and 8000 feet, always under rocks but under variable conditions of soil moisture and vegetation, e.g. dry soil with scattered juniper and pine or oak and pine, moist soil in a clearing near a hardwood forest, and moist soil in an open grassy area.

As is the case in other species of *Lasius,* observations on the food habits of *umbratus* are entirely fragmentary and anecdotal.

Umbratus is generally thought to be subterranean and to subsist primarily on the excreta of aphids and coccids, since these insects are often found in great numbers in the galleries with the ants (cf. Donisthorpe, 1927, and Gregg, 1944). However, in Holland, Stärcke (1937) has observed workers foraging aboveground at night and carrying insects to the nests presumably for use as food. Brown (pers. commun.) has also observed workers aboveground on cloudy days in Pennsylvania.

A number of nuptial flights recorded by Donisthorpe (1927), Crawley (1915), and Eidmann (1926) suggest a long flight season in Europe, extending from as early as August 8 (Crawley) to as late as October 7 (Eidmann). However, there is again no way of knowing whether these records might not represent the overlapping periods of the two species *umbratus* and *rabaudi*. Winged queens, determined by me as authentic *umbratus*, have been taken in Europe on the following dates: IV-4, V-11, VI-9, VI-12, VII-24, VII-31, VIII, VIII, VIII-(15-20), VIII-22, VIII-28, IX-3, IX-10, IX-13, IX-16, IX-17, IX-29; these do not involve any apparent geographic trend and by themselves may indicate an unusually long flight period.

The situation in North America is somewhat similar. I have observed queens in flight in the environs of Boston, Mass., in September during two recent seasons. Lone dealate queens were found wandering above ground at Cambridge, Mass., on September 5, 1952, and October 2, 1953, and at Plantagenet, Ontario, on June 30, 1952. Dates on which winged forms have been taken alone or *in nido* cover the same period, as shown by the following random sample: VI-28, VII-8, VII-27, VIII-1, VIII-8, VIII-13, VIII-13, VIII-18, VIII-20, VIII-31, IX-1, IX-5, IX-9, IX-27, X-14, X-28, X-29. Since there are no known sibling species to complicate the picture in North America, the data here suggest that on this continent at least umbratus has an unusually long nuptial season.

There is no evidence to indicate that the reproductives of *umbratus* build aerial swarms during their nuptial flights, as do those of *niger* and *flavus*, although this does not preclude the possibility. Eidmann (1926) observed queens of *umbratus* (or *rabaudi?*) flying singly in Germany, and I have observed definitely determined *umbratus* queens flying singly on two occasions in the Boston area.

Donisthorpe (1927), Crawley (in Donisthorpe, *ibid.*), Gösswald (1938), and Hölldobler (1953) have reported in detail on the colony founding behavior of "*umbratus*" and "*mixtus*". The normal hosts are *L. niger* and *L. alienus*. Under both field and laboratory conditions dealate *umbratus* queens attack host workers as they encounter them away from the nests, seizing them up the mandibles and carrying them about as they resume foraging. Their victims are usually killed by this treatment and may eventually be eaten. With the fulfillment of this *Mordinstinkt,* as Hölldobler calls it, and the presumed acquisition of the host odor, the queens are ready and able to enter host colonies, although they may be subjected to further attack before acquiring final acceptance. Unfortunately, the authors who have witnessed this phenomenon failed to make a convincing distinction between *umbratus* and *rabaudi*, and specimens were not saved to allow corroborative determinations during the present revision.

During the falls of 1952 and 1953 I collected numerous dealate *umbratus* queens at Cambridge, Mass., and tried introducing them into colonies and colony fragments of *sitkaensis, alienus,* and *neoniger,* but never obtained a complete adoption and saw no evidence of the *Mordinstinkt* behavior. I have also worked on the theory that the *umbratus* may join recently fecundated host queens, since both host and parasite queens are often found in species-pure groups under rocks following nuptial flights. Various attempts to bring *umbratus* and *neoniger* queens together, including placing them in the same chamber while chilled, have so far failed; the reason may be, however, that *neoniger* is not a natural host. I would like to suggest, on what admittedly constitutes negative evidence, that behavior in the population I studied may differ from that in the European populations. If true, this could be due either to geographic variation or to the fact that the European authors were using *rabaudi* instead of *umbratus*. Only additional research accompanied by careful determinations will settle the matter.

Niger and *alienus* probably serve as hosts of *umbratus* in North America as they do in Europe. I have seen two mixed *niger-umbratus* nest series from Ute Park, New Mexico (A. C. Cole leg. and Coll., MCZ) and one *alienus-umbratus* series from Beatty, Pennsylvania (Schmitt leg.; MCZ). The Beatty *um-*

bratus are minimas. Buren (1944) found a single dealate "*aphidicola*" queen with a depauperate colony of "*flavus nearcticus*", but to my knowledge there has been no additional evidence forthcoming that this or any other *Chthonolasius* uses species of *Cautolasius* as hosts.

SYNONYMY. *Formica mixta* Nylander. Holotype, a dealate queen in the Helsinki Museum. The status of this important synonym has already been fully discussed in the section on geographic variation.

Formica aphidicola Walsh. The location of the types of this form is unknown. They may be in the Academy of Natural Sciences, Philadelphia, although I was unable to find them during a brief visit there. As I have already shown, the North American population tends to differ as a unit in queen body size and worker eye size but the overlap in these two characters is too great to allow even a conventional subspecific division.

Formica affinis Schenck. What are probably the long-forgotten syntypes of this form have been located in the section of the Schenck Collection owned by the University of Marburg. Specimens sent me by Prof. E. Kessel of the Zoologisches Institut are labelled "Lasius affinis Sck" but lack locality or type data. However, these are the only specimens in the collection determined as *affinis*, all three castes are represented as was stated to be the case with the type series, and all fit Schenck's original description. The many commentaries written in the past on the status of *affinis* (along with the series I have seen determined as this species by various European authorities) leave no doubt that *affinis* must stand or fall on the single presumed distinction that the petiolar scale is proportionately higher in *affinis* than in the typical *umbratus*. That it must fall has been determined by measuring the scale height against the head width of European series of *umbratus*. The putative *affinis* queen syntype has a scale height (measured from the bottom of the ventral lobe to the dorsal crest) of 1.08 mm. and a HW of 1.64 mm. *Umbratus* series with the same approximate HW (1.58-1.73 mm.) showed every gradation in scale height from 0.83 mm. to 1.10 mm. It is obvious that "*affinis*" represents only one extreme in this highly variable *umbratus* character. The queen syntype is also notable in having a deeply emarginate scale, but as previously noted this is also within the normal *umbratus* range of variation. (See Pl. 2, Fig. 1.)

Lasius umbratus var. *mixto-umbratus* Forel and *L. umbratus* var. *affino-umbratus* Donisthorpe. These two varieties were erected to cover intermediates between the two major variants *mixtus* and *affinis* and therefore automatically fall into the synonymy.

Lasius umbratus var. *exacutus* Ruzsky. This variety was based on workers with high, tapering, emarginate petiolar scales and hairy scapes and tibiae. The lack of types notwithstanding, it is probably safe to conclude from the description alone that *exacutus* falls within the normal range of variation of *umbratus*. At the same time, of course, there is no way of determining whether this and other forms under *umbratus* which have been based on the worker caste alone are really *umbratus* and not *rabaudi,* since no characters have been found to separate the workers of these two sibling species.

Lasius umbratus var. *przewalskii* Ruzsky. Like *exacutus* this variety is characterized by a high, tapering petiolar scale. It differs from *exacutus* in that the dorsal crest is less deeply emarginate, and the scapes and tibiae lack standing hairs. Like *exacutus*, it is probably well within the normal range of variation of the *umbratus* group. It is not clear how Ruzsky thought he could distinguish *exacutus* and *przewalskii* from *affinis,* since they share the same principal diagnostic character, but this is of little consequence so long as the names remain in synonymy.

Formicina umbrata distinguenda Emery. This is the name applied to larger southern European queens lacking standing tibial hairs and will have priority if some future taxonomist feels the need to apply a trinomen to the southern population.

Formicina belgarum Bondroit. Reduced to a variety by Stärcke, this form is based on trivial characters in pilosity, petiole outline, color, etc., and seems to be well within the range of normal variation of the European population.

Lasius bicornis var. *citrina* Emery. Lectotype by present selection, a worker in the Emery Collection labelled ''Monte Gargano 1907''. This specimen is a typical *umbratus* (or *rabaudi*), with the petiolar emargination forming an angle of about 100°, easily within the range of variation of *umbratus*. The naming of this form undoubtedly resulted from Emery's erroneous conception of the species line separating *umbratus* and *bicornis.*

Lasius umbratus var. *viehmeyeri* Emery. The head shape of the queen figured by Emery is not far divergent from what would be expected in very large specimens conforming to normal allometric variation. The shining sculpture mentioned by Emery is inconsistent with the known allometric trend in *umbratus,* but otherwise *viehmeyeri* does not seem to differ significantly from this species.

Lasius silvestrii Wheeler. The status of this form has been discussed in the section on geographic variation.

Lasius viehmeyeri var. *dalmatica* Stärcke. New and convincing evidence for the specific status of *viehmeyeri* must be produced before *dalmatica* can be considered as anything more than a trivial variant of *umbratus.*

Lasius umbratus var. *hirtiscapus* Stärcke. This is undoubtedly the extreme hirsute form of the northern population previously discussed in the section on geographic variation.

Lasius umbratus distinguendus var. *cereomicans* Stärcke. This is a trivial variety established on what appears from the description to be a fortuitous, non-genetic character.

Lasius silvestri [!] var. *osakana* Santschi. The status of this form has already been discussed in the section on geographic variation. The holotype is nearly identical with typical northern European queens of *umbratus.*

Chtonolasius [!] *affinis* var. *nyárádi* Röszler. On morphological evidence alone, this variety must fall into the synonymy along with *affinis.*

Lasius umbratus epinotalis Buren. I have been able to examine a single paratype of this form in the Creighton Collection. Contrary to the statement of Creighton (1950), eye size in this specimen does not link it to *subumbratus,* but rather places it in the center of the EW-HW regression zone of the North American population of *umbratus* as plotted in Figure 17. Furthermore, differences in size, antennal conformation, propodeum shape, and pilosity as given by Buren and Creighton have proven upon critical examination to be trivial or non-existent. At the most, *epinotalis* has unusually sparse gastric pubescence for an *umbratus,* but it is still within the extreme range of variation shown by that species. Examination of additional material from Iowa (King Coll.) has shown that *epinotalis* is not a representative of any significant geographic trend in this character.

LASIUS RABAUDI (Bondroit)

(Subg. *Chthonolasius*)

Formicina rabaudi Bondroit, 1917, Bull. Soc. Ent. Fr., **86**: 177; queen; original description. Type locality: Amélie-les-Bains, Pyrénées-Orientales, France.

Formicina meridionalis Bondroit, 1919, Ann. Soc. Ent. Belg., **88**: 143; original description. Type locality: Aveyron, France. NEW SYNONYMY.

Lasius tibialis Santschi, 1926, Bull. Soc. Sci Nat. Maroc, **16**: 208; queen; original description. Type locality: Grand Atlas Mountains, Morocco. NEW SYNONYMY.

DIAGNOSIS. A common Palaearctic species very close to *umbratus* and safely distinguishable only in the queen caste.

Queen. (1) Scapes and tibiae conspicuously flattened, so that the minimum width of the scape at the midpoint is 0.10 mm. or less (Fig. 15).

(2) Funicular segments tending to be proportionately longer than in *umbratus*. In the *rabaudi* series examined, funicular segment III varied 1.47-1.87 × longer than broad, while an equivalent sample of Eurasian *umbratus* varied 1.00-1.50 × longer than broad, with only one specimen exceeding the *rabaudi* minimum of 1.47 ×.

(3) The shape of the petiole characteristic, and less variable than in *umbratus:* in frontal view subquadrate, nearly as broad at the dorsal crest as at the level just above the frontal foramen, and with a rounded to angulate dorsal emargination. European series have concave to straight lateral margins; Japanese series may have convex margins in addition.

Worker. (1) The most reliable queen character, the flattening of the scape, seems to be reflected in the worker, but there is considerable overlap between the two species, and probably a majority of worker series unaccompanied by queens cannot be certainly placed. Series of *umbratus* accompanied by queens are characterized as follows: in workers with maximum midpoint scape width of 0.10-0.12 mm., the minimum midpoint width was always 0.08 mm. or more. In the two series of *rabaudi* accompanied by queens (''Morogi-Mura'' and Roermond) the minimum width was distinctly less than 0.08 mm. However, other series unaccompanied by queens, and therefore not determinable by reference to the *rabaudi* type, completely overlapped determined *umbratus* and extended far below the identified *rabaudi* series, to minimum width 0.06 mm.

(2) The "Morogi-Mura" and Roermond series and others with greatly flattened scapes also had abundant standing hairs on the scapes, which character is frequent in *umbratus* only in northern Eurasian samples.

Male. Males associated with very flat-scaped workers from Roermond are rather small compared to *umbratus* (HW about 0.98 mm.) and show certain expected allometric differences in mandibular and petiolar structure, but in this and every other character they are within the extreme range of variation of *umbratus.* There is no appreciable flattening of the scapes.

HOLOTYPE. An alate queen in the Bondroit Collection. HW 1.73 mm., SL 1.53 mm., SI 89; maximum width of scape at midlength 0.15 mm., minimum width 0.08 mm.; length of third funicular segment 0.17 mm., width 0.11 mm. The relative length of the antennae and the length of the cephalic hairs slightly exceed those of any other European series examined but are within the range of variation of the Japanese series and nearly identical with the *tibialis* holotype from North Africa. The petiolar scale is typical of the species; the sides are straight in frontal view. There can be little doubt that, despite its somewhat atypical nature, this specimen belongs to the same species later called *meridionalis* by Bondroit and Stärcke. Bondroit's opinion concerning the holotype's resemblance to *Dendrolasius* is manifestly erroneous.

GEOGRAPHIC VARIATION. Nearly all European queens examined have the same frontal petiolar outline, shallow emarginate dorsal border and feebly concave sides. The types of *rabaudi*, from southern France, and *tibialis,* from North Africa, have petioles with straight sides and slightly deeper dorsal emarginations. A queen from Ashoromura, Hokkaido, and one from Hikosan, Kyushu, have concave sides, while other Japanese series have straight to feebly convex sides. The Japanese series also show variation in the dorsal emargination from shallow-rounded to moderate-angulate. The Japanese series and *rabaudi* and *tibialis* holotypes have proportionately longer antennae.

The Japanese series have denser body hair than the European and as a rule hairer scapes, although the Roermond series exceeds one Hikosan queen in this respect. In both the queen and worker the standing hairs on the head and gaster tend to be proportionately longer in the Japanese series than in the European.

DISTRIBUTION. Queens determined as *rabaudi* and included in the plot in Figure 15 came from the following localities. ENGLAND: "Inghilterra Crawlei" (from Finzi Coll. in MCZ). SWEDEN (all Bo Tjeder leg., Forsslund Coll.); Kåseberga, Kristianstad, VII-22-1950; Löderup, Kristianstad, VII-21-1950; Högsrum, Öland. HOLLAND: Den Dolder, three series, VII-15-1943, VII-24-1944, VII-25-1944 (A. Stärcke leg.; Holgersen Coll.); Roermond, VII-27-1947 (J. K. A. van Boven leg.; USNM). FRANCE: Aveyron (*meridionalis* holotype); Amélie-les-Bains, eastern Pyrenees (*rabaudi* holotype). SWITZERLAND: Zermatt, VIII-12-1919 (H. Kutter leg. and Coll.). AUSTRIA: Vienna (MCZ). ITALY: Lavarone, Venezia Tridentina (MCZ); Trieste (MCZ); Barcola, near Trieste (MCZ). YUGOSLAVIA: Dubrovnik (Novak leg.; MCZ). MOROCCO: Grand Atlas Mountains (*tibialis* holotype). HOKKAIDO: Ashoromura, VIII-9-1949 (R. Matsuda leg.; Yasumatsu Coll.). HONSHU: Tokyo, VI-6-1931 and VI-20-1931 (L. Gressitt leg.; MCZ). KYUSHU: Hikosan, 2 series VII-6-1939, VIII-5-1940 (Yasumatsu leg. and Coll.); Sobosan, VII-16-1931 (Esaki and Fujino leg.; Yasumatsu Coll.). SHIKOKU: "Morogi-Mura", VI-25-1952 (Okamoto leg. and Coll., MCZ); Yoshino (Okamoto leg. and Coll.). Workers unaccompanied by queens, but with greatly flattened scapes, have been recorded from Roermond (with males, VII-17-1947; van Boven leg.; MCZ); Hikosan, Kyushu (Yasumatsu leg. and Coll.); Hirooka and Mt. Kajigamori, Shikoku (Okamoto leg. and Coll., MCZ).

ECOLOGY. Stärcke (1937) has obtained the experimental adoption of *rabaudi* (=*meridionalis*) queens by *L. niger* workers. Later observations by the same author suggest that *rabaudi* can serve in turn as the host for *L. fuliginosus* (see the section on ecology of that species).

SYNONYMY. *Formicina meridionalis* Bondroit. Holotype, a dealate queen in the Bondroit collection. HW 1.63 mm., SL 1.38 mm., SI 84; maximum width of scape at midpoint 0.16 mm., minimum width 0.09 mm.; length of third funicular segment 0.15 mm., width 0.10 mm. This specimen is somewhat more typical of the European population in relative antennal length and cephalic pilosity than is the *rabaudi* holotype.

Lasius tibialis Santschi. Holotype, a queen in the Santschi Collection. HW 1.73 mm., SL 1.54 mm., SI 89; maximum width of scape at midpoint 0.17 mm., minimum width 0.10 mm.; length of third funicular segment 0.18 mm., width 0.10 mm. This specimen is nearly identical in every respect with the *rabaudi* holotype.

LASIUS SPECULIVENTRIS Emery

(Subg. *Chthonolasius*)

Lasius speculiventris **Emery, 1893, Zool. Jahrb. Syst., 7: 641–642; worker, male; original description. Type locality: Caldwell, New Jersey.**

Lasius umbratus speculiventris**, Wheeler, 1910, Psyche, 17: 242.**

DIAGNOSIS. An eastern North American species closely related to *umbratus*, but differing by its very sparse gastric pubescence and tendency toward denser cephalic and appendage pilosity.

Worker. (1) Central area of exposed second gastric tergite, exclusive of the posterior strip, almost completely devoid of pubescence of any kind and with only a few widely scattered erect hairs, its cuticular surface extremely smooth and shining. The third and posterior tergites are usually very similar in this respect to the second, but the first tergite may have the bare area limited to a median longitudinal strip as narrow as one-fourth the width of the gaster (E. S. George Reserve, Mich.). Series at the opposite extreme (Caldwell, N. J.; Volo, Ill.; Chicago, Ill.) have no pubescence whatsoever on the gastric tergites except for thin zones along the posterior tergital margins.

(2) Standing appendage and cephalic pilosity ranging from extremely dense (scapes and legs covered with abundant, predominantly subdecumbent to erect hairs, and the margin of the head seen in full face from the mandibular insertions to the anterior borders of the eyes with more than 20 erect hairs) to less dense than the extreme hirsute form of *umbratus* (hairs on the scapes and legs mostly appressed-decumbent and seldom standing, and only one or two erect hairs along the genal contour). The type series exhibits the first extreme, and the Urbana, Ill., series, the second. There is no evident correlation between

the density of the cephalic and anterior appendage pilosity and the density of the gastric pubescence.

Queen. (1) Gastric pubescence as in worker. Dorsal surfaces of second, third, and fourth tergites exclusive of the posterior strips almost completely devoid of pubescence. Dorsal surface of first tergite covered with appressed pubescence except for a thin, longitudinal, median strip about 0.15 mm. in width.

(2) Scapes and legs hairier than in all North American *umbratus* seen but still within range of variation of Eurasian series, Scape densely covered with short, predominantly decumbent hairs. Femora and tibiae with dense appressed pilosity and scattered short but outstanding decumbent hairs.

(3) In all other aspects apparently identical to *umbratus.* Extreme HW range 1.53-1.62 mm.

Male. (1) At least the median longitudinal fourth of the second and posterior gastric tergites devoid of pubescence, its cuticular surface smooth and shining; in the type series the entire dorsal gastric surface is devoid of hairs and strongly shining.

(2) Standing hairs more abundant on the head and alitrunk than in North American *umbratus.* In the type series, but not in another series from Ramsey Co., Minn., erect hairs are abundant along the genal contour viewed in full face.

(3) Extreme HW range 1.00-1.21 mm.

LECTOTYPE. By present selection, a worker in the Museum of Comparative Zoology labelled ''Caldwell, N. J., Sept. 11 '88.'' Synnidotypes are in the Museum of Comparative Zoology, Emery Collection, American Museum of Natural History, and United States National Museum. The extreme nature of this series with respect to the rest of the species population has already been mentioned.

DISTRIBUTION. This species is widespread in the eastern United States and seems to be most common in the Great Lakes district. Following are all of the records accumulated during the present study. NEW JERSEY: Caldwell, Essex Co. (type series). PENNSYLVANIA: Lemont, Centre Co. (W. L. Brown leg.; Pennsylvania State University Coll.). ILLINOIS: Chicago (M. Talbot leg. and Coll., MCZ); New Lenox, Will Co. (Talbot leg. and Coll.); Volo, Lake Co. (Talbot leg. and Coll.). MICHIGAN: E. S. George Reserve, Livingston Co., winged queens collected as pupae VIII-1-1953 and preserved after eclosion VIII-10-1953 (Talbot leg. and Coll.); Ann Arbor (J. Dawson leg.; MCZ); East Lansing, winged queens IX-1899 (USNM); Litchfield, Hillsdale Co. (A. M. Holmquist leg.; USNM). MINNESOTA: Ramsey Co., winged queens and males VIII-25-1922 (A. T. Hertig leg.; USNM). IOWA: Iowa City (USNM). KANSAS: Douglas Co., winged queen, June (E. S. Tucker leg.; U. of Kans. Coll.). Series recorded by Cole (1940) from the Great Smoky Mountains of Tennessee as *speculiventris* have been re-examined and determined as *umbratus.*

ECOLOGY. Dr. Talbot has kindly supplied me with ecological notes on several of her collections. This species nests under a variety of conditions. At Volo it was taken in natural hummock in marshy ground near a larch-sphagnum bog. At New Lenox two colonies were found in a pasture, deep in the sod under rocks set in a dry ditch bank. At the E. S. George Reserve a huge colony was found beneath a layer of red woody soil under a dead standing tree in oak-hickory woods; the ants had galleried the roots of the dead trees into thin partitions.

LASIUS VESTITUS Wheeler
(Subg. *Chthonolasius*)

Lasius umbratus vestitus Wheeler, 1910, Psyche, **17**: 242; queen; original description. Type locality: Moscow, Idaho.

Lasius vestitus, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 425.

Lasius pilosus M. R. Smith, 1934, Ann. Ent. Soc. Amer., **27**: 384; worker; original description. Type locality: Moscow, Idaho (probably Moscow Mountain, near Deary, Latah Co.). NEW SYNONYMY.

DIAGNOSIS. A western North American species closely related to *umbratus* but easily distinguished in both the queen and worker castes by its unusual body pilosity.

Queen. (1) Entire body, including the gula, genae, and outer lateral margins of the mandibles, densely covered with long, predominantly erect, silky-yellow hairs. Those on the gaster exceptionally uniform in length and inclination, lending the gaster a brush-like appearance in side view; the longest hairs on the tergites are 0.25 mm., approximately the maximum width of the hind tibia midpoint. These tend to be sparser and shorter on the sides of the alitrunk than on the dorsum, not exceeding 0.14 mm. The numerous hairs set along the dorsal petiolar crest tend to be curved and many are even flexous. The scapes, femora, and tibiae with abundant shorter, predominantly subdecumbent-erect hairs on all surfaces. Entire body covered with dense, appressed pubescence.

(2) Total size averaging smaller than other *umbratus*-complex members, and appendages averaging proportionately longer. HW and SI of all available specimens are as follows: 1.37 mm., 89; 1.42 mm., 90; 1.42 mm., 86; 1.42 mm., 87; 1.43 mm., 89; 1.43 mm., 90; 1.44 mm., 88; 1.46 mm., 85; 1.46 mm., 89; 1.52 mm., SI not measurable.

(3) Body color uniformly medium brown, the appendages light brown.

Worker. (1) Exposed gastric tergites evenly covered with abundant, long, suberect-erect hairs; the longest over 0.12 mm., or exceeding four-fifths the maximum width of the hind tibia at its midlength. At least a few scattered standing hairs present on the scapes, femora, and tibiae.

(2) Size apparently about the same as in *umbratus;* PW range 0.66-0.73 mm.

The worker is generally very similar to the large, hairy Eurasian form of *umbratus*, differing slightly in the length of the body pilosity as exemplified in the above description of the gastric pilosity. At the same time it is strikingly different from the sympatric North American form of *umbratus* and can be separated at once by its possession of standing hairs on the scapes and tibiae.

HOLOTYPE. A queen in the Museum of Comparative Zoology, now in poor condition, with the head missing and much of the body pilosity broken down or worn off. Other queens in the same collection, however, show a detailed correspondence in all features that could be studied.

GEOGRAPHIC VARIATION. Workers from Moscow have a notably denser pilosity than others from Corvallis; seta count of the single measurable Moscow specimen is 13, seta counts of the measurable Corvallis workers are 2, 3, 5, and 11. This difference, however, is not manifested between the holotype, from Moscow, and queens from farther west.

DISTRIBUTION. *Vestitus* appears to be concentrated along the Pacific Coast, but extends eastward at least as far as western Idaho. CALIFORNIA: Lassen Pk. Trail, Shasta Co., winged queen VII-14-1947 (D. W. Adams leg.; USNM); Requa, Del Norte Co. (C. D. Duncan leg.; UMMZ). OREGON: Corvallis, workers II-10-1936, a winged queen V-24-1935 (G. Ferguson leg.; MCZ); Alsea Mountain, Benton Co., winged queen V-18-1947 (H. A. Scullen leg.; USNM); Rickreall, Polk Co., a winged queen VII-15-1933 (J. Schuh leg.; MCZ); Zigzag Glacier, Mt. Hood, winged queens VII-7-1927 (P. J. Darlington leg.; MCZ). BRITISH COLUMBIA: Forbidden Plateau, Vancouver Island, a winged queen VII-13-1935 (J. D. Gregson leg.; USNM); Nanaimo (E. C. Van Dyke leg.; CAS). IDAHO: Moscow (*vestitus* holotype, *pilosus* nidotypes).

SYNONYMY. *Lasius pilosus* M. R. Smith. There can be little doubt that *pilosus* represents the worker caste of *vestitus*. Although never associated in the same nest series, both have been taken at the same two localities, Moscow and Corvallis, within a relatively small section of North America in which other *Chthonolasius* are rare or absent. In July, 1952, I spent two days at the type locality searching in vain for this species. Most of the area around Moscow is under heavy cultivation, but a large stand of forest still exists on Moscow Mountain, and this is very likely the origin of the *pilosus* types, as suggested by Smith. On Moscow Mountain I collected intensively on the southern slope from pine-larch forest around 3000 feet, up through a dense *Lasius sitkaensis* population in pine-fir forest, to the summit at 5500 feet. No species of *Lasius* other than *sitkaensis* were encountered during this time.

LASIUS SUBUMBRATUS Viereck
(Subg. *Chthonolasius*)

Lasius umbratus subumbratus Viereck, 1903, Trans. Amer. Ent. Soc., **29:** 73; queen; original description. Type locality: Beulah, San Miguel Co., New Mexico.

Lasius subumbratus, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 424.

DIAGNOSIS. A close relative of *umbratus* sympatric with that species over most of its range from the maritime provinces of Canada to western North America and best distinguished from it by differences in body pilosity.

Queen. (1) Pilosity on anterior three gastric tergites very long (maximum length 0.24-0.27 mm., or approximately the maximum width of the hind tibia at midlength), silvery yellow, and predominantly decumbent-subdecumbent. Similar erect hairs form a fringe around the entire dorsal and lateral margins of the petiole; these are often curved toward their tips. Pilosity of alitrunk mostly limited to the dorsal surface, from the posterior margin of the pronotum to the dorsal face of the propodeum, averaging shorter than on the gaster and petiole, maximum length about 0.24 mm., subdecumbent to erect, often curved or sinuate. Pilosity of head mostly limited to the occipital zone, averaging shorter than on the alitrunk, maximum length about 0.18 mm., predominantly subdecumbent-suberect and often curved.

(2) Averaging larger and with proportionately longer ap-

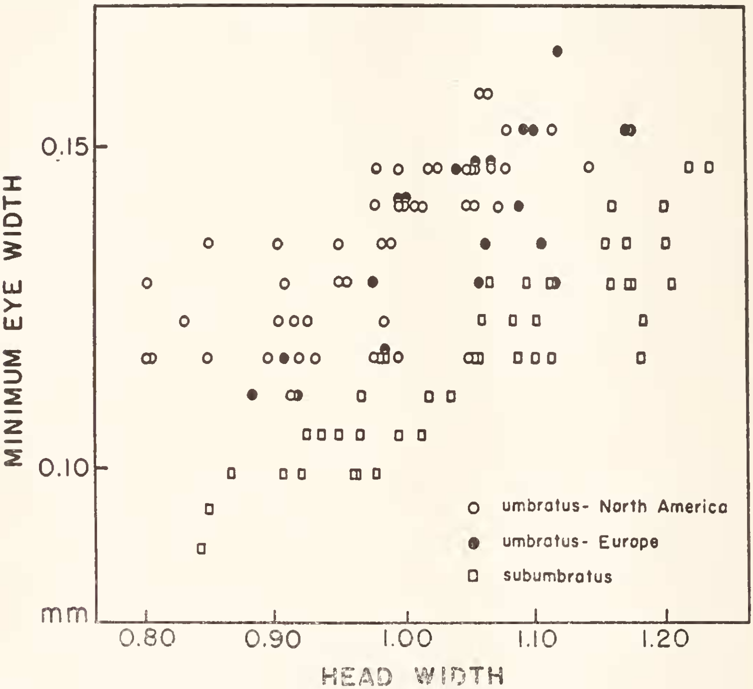

Fig. 17. Worker head width-eye width relationships in *L. subumbratus* and two geographic samples of *L. umbratus*. Further explanation in text. Nest series chosen at random; no more than two workers per series were measured.

pendages than the sympatric North American population of *umbratus*. Extreme range of HW with attendant SI of series examined 1.56 mm., 85; 1.74 mm., 83.

(3) Color averaging lighter than in *umbratus*. Body typically medium yellowish brown, head somewhat lighter; appendages light yellowish brown.

Worker. (1) Gastric pilosity longer and denser than in *umbratus*. The hairs on the first tergite with a maximum length of about 0.10 mm., or about 0.6 × the maximum width of the hind tibia at its midlength, mostly decumbent-subdecumbent (occasionally tending to suberect), and dense enough for the individual hairs to overlap one another widely. Scapes, femora, and tibiae with dense, predominantly decumbent pubescence and occasional standing hairs (*umbratus* in all populations with sparser pubescence, often appressed, and the North American population always lacking standing hairs). Gaster with very sparse pubescence, not obscuring in any way the shining cuticular surface.

(2) Eyes smaller than in North American *umbratus*, the HW-EW regression zones of the two species well separated, although no single absolute measurement will suffice to separate all the series. The Eurasian population of *umbratus* connects and overlaps the two (Fig. 17).

(3) Size averaging larger than in *umbratus*. PW range 0.55-0.85 mm.

(4) Body and appendages uniformly medium yellow, lighter than most North American *umbratus* and *minutus*.

Male. (1) Gastric pilosity similar to that of worker in form and inclination, but sparser, more often subdecumbent, and showing only limited overlap between individual hairs; maximum length of hairs about 0.13 mm., or 0.9-1.1 × the maximum width of the hind tibia at midlength. Maximum length of the hairs of the posterior two-thirds of the clypeus 0.12 mm., or slightly less than 0.10 × the HW.

(2) Averaging larger than in *umbratus;* maximum range in all series studied 1.05-1.17 mm.

(3) Genitalia similar in all respects to those of *umbratus*.

HOLOTYPE. A winged queen in the Academy of Natural Sciences, Philadelphia, in good condition and showing all of the characters used in the diagnosis above. A paratopotype queen, recently compared with the holotype, is in the Museum of Comparative Zoology.

DISTRIBUTION. Several hundred workers, queens, and males have been examined from the following localities. NOVA SCOTIA: Digby (J. Russell leg.; MCZ); Hunter Creek, Baddeck, winged queen VII-22-1936 (T. N. Freeman leg.; USNM); Bedford (W. Reig leg.; MCZ). MAINE: Bailey Island, near Brunswick (spruce woods) (K. Christiansen leg.; MCZ). MINNESOTA: "Itasca Park", winged queens VIII-14-1933 (L. W. Orr leg.; USNM). NORTH DAKOTA: Silvista, Walsh Co. (W. E. LaBerge leg.; G. C. Wheeler Coll., USNM); Devils Lake (C. Thompson leg.; UMMZ); Grand Forks (L. Monda leg.; G. C. Wheeler Coll.); SASKATCHEWAN: Regina (H. B. Leech leg.; Cole Coll., MCZ, USNM). IDAHO: Bloomington Lake, Franklin Co. (B. Malkin leg. and Coll., MCZ). MONTANA: Fish Creek Ranger Station, Glacier National Park (W. S. Creighton leg. and Coll.); Glacier National Park (R. A. Cooley leg.; MCZ); Belt, Cascade Co., dealate queen VIII-29-1933 (Creighton leg. and Coll.). WYOMING: Firehole River, Yellowstone Park, 7600 feet, winged queen VII-21-1928 (J. McDunnough leg.; USNM); Jenny Lake, Grand Teton National Park (V. M. Tanner leg.; USNM); Devils Tower National Monument (Malkin leg. and Coll., MCZ). COLORADO: Steamboat Springs, Routt Co., winged queen VII-1-1943 (CAS); Longs Peak Inn, 9000 feet, winged queen VII-15-1926 (E. C. Van Dyke leg.; CAS). WASHINGTON: Deer Park, Spokane Co., winged queens VIII-1-1938. NEVADA: Lehman Caves, Mt. Wheeler (Creighton leg. and Coll.). UTAH: Timpanogos Peak, Utah Co. (O. H. Swezey leg.; CAS); Shingle Creek, Uinta Mts. (Creighton leg. and Coll.); Mirror Lake, Uinta Mts., 11,000 feet, winged queen VIII-5-1933 (Creighton leg. and Coll.); Lake Blanche, 10,000 feet (A. W. Grundmann leg.; Cole Coll., MCZ); Monticello, Blue Mts. (Creighton leg. and Coll.); Bryce Canyon (Creighton leg. and Coll.); Long Valley Junction, Kane Co., winged queens and males VII-24-1952 (E. O. Wilson leg.; MCZ); Warner Ranger Station, La Sal Mts. (Creighton leg. and Coll.). ARIZONA: San Francisco Peaks, near Flagstaff (Wilson leg.; MCZ); Bear Wallow to Mt. Lemmon, and Mt. Lemmon, Santa Catalina Mts. (W. M. Wheeler leg.; MCZ); Shannon Forest Camp, Graham Mt. (Malkin leg. and Coll., MCZ); Rustler Park, Chiricahua

Mts. (Malkin leg. and Coll., MCZ); Ramsey Canyon, Huachuca Mts. (Creighton leg. and Coll.). NEW MEXICO: 18 miles east of Taos, 8000 feet (A. C. Cole leg. and Coll., MCZ); 5 miles east of Eagle Nest, Colfax Co., 8600 feet (Cole leg. and Coll., MCZ); Little Tesuque Canyon, near Santa Fe, 9000 feet (Cole leg. and Coll., MCZ); Tesuque Canyon, 10,000 feet, winged queens and males with workers (Cole leg. and Coll., MCZ); 14 miles south of Mescalero, Lincoln National Forest, 7925 feet (Cole leg. and Coll., MCZ).

ECOLOGY. Cole's New Mexican collections (see above) were made under stones in a variety of habitats, including a dry, open slope, an alpine meadow, and spruce-aspen, spruce-pine, and pine-aspen forests. Wheeler (1917b) found it common at Cloudcroft, New Mexico, under stones in pine forest. I found two colonies in pine-fir forest on a southern slope of the San Francisco Mountains of Arizona, one under a stone and one under a rotting log. In the southern Rocky Mountains *subumbratus* is clearly a high-elevation species; thus far it has been found only well above the lower elevational limits of sympatric populations of *sitkaensis*, *neoniger*, *crypticus*, and *sitiens*, and it ranges at least to the upper elevational limits of these species. In New Mexico Cole encountered it between 7400 and 10,000 feet, and at Cloudcroft Wheeler was unable to find it below 9000 feet. My Arizona colonies were found at about 8000 feet.

Wheeler's studies at Cloudcroft (1917b) leave no doubt that *subumbratus* is a temporary social parasite of *L. sitkaensis*. The alternate host, "*L. neoniger*," which he found nesting in open, dry situations, may be *sitkaensis* also. I have found nothing but *sitkaensis* in his collections from this locality, and this species was the only member of the subgenus encountered during my own brief visit there. According to Wheeler, *subumbratus* is abundant enough at Cloudcroft to flood the *sitkaensis* nests with queens at the time of the nuptial flight. At one spot after a nuptial flight (occurring July 6 or 7) he found dealate *subumbratus* queens in nearly every nest of the host species uncovered. He observed that these queens approach the *sitkaensis* workers in a conciliatory manner, that they are often rebuffed at first, and that they sometimes hide in the vicinity of brood piles prior to adoption. He saw one queen in the act of stealing a host pupa and another carrying an uninjured host worker.

The latter incident is reminiscent of the conditioning behavior of *umbratus* more recently described by several European authors (*q.v.*). Several *sitkaensis* colonies with recently adopted parasite queens were found, as well as two colonies containing workers of both species. From these observations Wheeler drew the conclusion that the *subumbratus* queens are by nature conciliatory, but still find it necessary to acquire some amount of the host nest odor in order to secure final adoption.

Additional evidence is available to indicate that *sitkaensis* is the principal, if not the only, host. Cole has found mixed *subumbratus-sitkaensis* colonies at Tesuque Canyon and Eagle Nest, New Mexico; the parasite workers from the latter locality are minimas and much smaller than the associated host workers. In another nest at the second locality a single dealate *subumbratus* queen was found with *sitkaensis* workers. Finally, there is in the Museum of Comparative Zoology a series of 6 dealate *subumbratus* queens associated with *sitkaensis* (Bedford, Nova Scotia; W. Reig leg.; MCZ).

Lasius minutus Emery
(Subg. *Chthonolasius*)

Lasius umbratus minutus Emery, 1893, Zool. Jahrb. Syst., **7**: 641; worker; queen, male; original description. Type locality: New Jersey, by designation of Creighton (1950).

Lasius bicornis minutus, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 421.

DIAGNOSIS. A distinctive North American species most easily recognized by the small size and unusual pilosity of the queen. (See under diagnosis of *L. bicornis* for a more detailed comparison with that species.)

Queen. (1) Smaller than *umbratus* and *bicornis*. HW of all available series ranging 1.02-1.17 mm.

(2) Entire body covered with long, coarse hairs, the longest on the first two gastric tergites longer than the greatest width of the hind tibia at its midlength. Scapes completely bare of standing hairs; tibiae bare except for a few decumbent hairs along the flexor margins of the hind tibiae.

(3) Petiole in frontal view shallowly and angularly emarginate, with very broadly rounded dorsolateral corners.

(4) The scape rounded in cross-section.

Worker. Similar to *umbratus* in habitus, but smaller and with distinctive pilosity and petiole shape.

(1) Apparently averaging and ranging smaller than *umbratus;* extreme PW range 0.52-0.69 mm.

(2) Entire body covered with long, coarse standing hairs, the longest on the alitrunk and gastric tergites at least 0.6 × as long as the maximum width of the hind tibia midpoint and usually much longer. At the same time, the scapes and tibiae completely bare except for a few decumbent hairs along the flexor margins of the tibiae. Pubescence abundant and strongly appressed.

(3) The petiole, measured in frontal view from the level of the dorsal border of the posterior foramen to the level of the dorsolateral corners, longer than its maximum width in frontal view, and usually with a distinctive shape: tapering from the broadest level (just above the foramina) to the dorsal crest and often expanding again just at the level of the crest; the dorsal margin distinctly but shallowly emarginate (Pl. 2, Fig. 4).

(4) The scape rounded in cross-section.

Male. (1) Smaller than *umbratus* and other *umbratus* complex members. HW range of limited sample measured 0.80-0.92 mm.

(2) Long, coarse standing hairs abundant over body surface, the longest on the clypeus exceeding 0.15 mm., or greater than one-sixth the head width; the longest on the first gastric tergite 0.15 mm., or 1.6 × the maximum width of the hind tibia at its midlength.

SYNTYPES. Three nidotopotype workers in the Museum of Comparative Zoology ("N. J./Aug. 25 '85/Pergande") correspond well to syntype workers borrowed from the Emery Collection ("Kittery Point, Me./Aug. '91/no. 285"). I have declined to designate a lectotype because of the good possibility that this former series was not in Emery's hands at the time of original description, but there can be no doubt that the name has been correctly placed.

DISTRIBUTION. This species is evidently limited to eastern North America. Following are all of the records accumulated during the present study. NOVA SCOTIA: Pleasantfield (W. H. Prest leg.; MCZ). MAINE: Kittery Point (syntypes from Emery Coll.). NEW HAMPSHIRE: East Jaffrey (R. E. Danforth leg.; MCZ). MASSACHUSETTS: Forest Hills, winged queens and males VIII-12-1910 (M. Tanquary leg.; MCZ); Stony Brook Reservation (W. S. Creighton leg. and Coll.); Lexington, dealate queen VI-22-1953 (R. H. Lippitt leg.; MCZ); Springfield (MCZ); Natick, winged queen IX-20-1923 (MCZ). CONNECTICUT: Colebrook (W. M. Wheeler leg., MCZ). NEW YORK: Flushing (K. W. Cooper leg.; MCZ). NEW JERSEY: Caldwell, Essex Co. (USNM). PENNSYLVANIA: Oxford, Chester Co., and Ottsville, Bucks Co. (W. L. Brown leg.; Pennsylvania State University Collection). INDIANA: Steuben Co. (R. L. Morris leg.; USNM). OHIO: Holland, Lucas Co., male VIII-20?-1932 (M. Talbot leg. and Coll., MCZ). ILLINOIS: Volo, Lake Co. (Talbot leg. and Coll., MCZ); Wauconda, Lake Co. (Ross and Sanderson leg.; INHS); Antioch, Lake Co. (Ross and Sanderson leg.; INHS); Chicago (MCZ); Rockford (MCZ). MICHIGAN: Livingston Co. (Talbot leg. and Coll., MCZ). MINNESOTA: Hennepin Co. (C. T. Schmidt leg.; USNM). VIRGINIA: Vienna, Fairfax Co. (J. C. Bridwell leg.; USNM).

ECOLOGY. Notes accompanying the above records indicate that *minutus* prefers to nest in sphagnum bogs and swampy meadows but will also move into open, dry forest. It has been taken most often in mounds or masonry domes in open areas, and only once (Steuben Co., Ind.) in a log. Brown (pers. commun.) has supplied me with complete notes on his Pennsylvania collections. South of Oxford, near the Pennsylvania-Maryland border, he found a population of this species nesting in masonry domes on the open grassy floor of a tongue of pitch pine woods. These domes measured between about 8 and 18 inches in height and about 2 feet in base diameter, had peculiar bulging sides, and were overgrown with short grass. Similar domes were found in a population at Ottsville along the border of an old pasture and oak-hickory woods. At both localities workers were rather scarce in the nests, and at Ottsville some of the domes were inhabited by *Formica fusca* instead.

A clue to the host species of *minutus* is supplied by the following note accompanying a series in the United States National Museum: "N. J./Aug. 15 '85/in hickory stem with L. alienus." The nesting site is one typical for *alienus*, and the determination in this case was probably correct.

LASIUS BICORNIS (Foerster)
(Subg. *Chthonolasius*)

Formica bicornis Foerster, 1850, Hymenopterologische Studien, no. 1, pp. 41–43; queen; original description. Type locality: Aachen, Germany.

Lasius bicornis oertzeni Forel, 1910, Ann. Soc. Ent. Belg., **54**: 26–27; worker, queen, male; original description. Type locality: Peloponnesus, Greece. NEW SYNONYMY.

Lasius oertzeni, Stärcke, 1937, Tijdschr. Ent., **80**: 56.

Formicina microgyna Bondroit, 1918, Ann. Soc. Ent. Fr., **87**: 33–34; queen, male; original description. Type locality: Saint Affrique, Aveyron, France, by present selection. NEW SYNONYMY.

Lasius bicornis var. *neapolitana* Emery, 1922, Bull. Soc. Ent. Ital., **54**: 13; queen, male; original description. Type locality: Naples, Italy. NEW SYNONYMY.

Acanthomyops bicornis kashmirensis Donisthorpe, 1930, Ann. Mag. Nat. Hist., (10) **5**: 225–226; queen, male; original description. Type locality: Kashmir. NEW SYNONYMY.

DIAGNOSIS. A rare Eurasian species somewhat similar in habitus to the North American species *minutus* but showing profound differences in the petiolar outline and pilosity. The following diagnosis is based on part of the type series of *oertzeni* and *microgyna* (including specimens labelled as syntypes of *microgyna* but coming from Saint Sever, Aveyron, a locality not mentioned in the original description), on a single unlabelled worker from the Mayr Collection, and on descriptions and figures (by Dr. H. Bischoff) of two queens in the Berlin Museum.

Queen. (1) Smaller than *umbratus* but considerably larger than *minutus*. HW of *oertzeni* lectotype 1.34 mm.; *microgyna* lectotype 1.25 mm., syntopotypes 1.24 and 1.26 mm., Saint Sever "syntypes" 1.22 and 1.29 mm.; a queen from the Taurus Mountains, Turkey (Berlin Museum), 1.34 mm. (measured by H. Bischoff).

(2) Long standing hairs abundant over the alitrunk, approaching the *minutus* condition, but sparser on the head and gastric tergites. In full face, the number of hairs projecting beyond the occipital contour is 4 in the *oertzeni* lectotype, 6 in the *microgyna* lectotype, 5 and 7 in the *microgyna* syntopotypes, and 6 and 7 in the Saint Sever specimens; the number in *minutus* is commonly 30 or more. In perfect side view, the first gastric tergite of the *oertzeni* lectotype shows only 15 standing hairs

projecting beyond its profile, the *microgyna* lectotype 12, and *microgyna* syntopotypes 10 and 14, the St. Sever specimens 13 and 15, and a specimen from Hanau (Berlin Museum) 7; the typical number for *minutus* is 25 or more. In *bicornis* the pilosity of the first gastric tergite is limited mostly to the anterior slope and extreme posterior strip; in *minutus* it is evenly distributed over all of the tergital surface except for the anteriormost part of the anterior slope. The body hairs are proportionately shorter than in *minutus*. The longest hairs of the first and second gastric segments shorter than the maximum width of the hind tibia at its midlength (in the *oertzeni* lectotype, for instance, maximum hair length is 0.17 mm., tibia width is 0.21 mm.). At the same time, *bicornis* resembles *minutus* in having the scapes and legs completely bare of hairs except for a few scattered along the flexor margins of the femora.

(3) The petiole in frontal view slender, tapering dorsally; deeply emarginate, so that the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination is distinctly greater than the width of the emargination taken across the midpoint of the depth measurement (Pl. 2, Fig. 2).

(4) Scapes flattened as in *rabaudi;* in the *oertzeni* lectotype, the maximum width at the midpoint is 0.14 mm., the minimum width only 0.07 mm. At the same time, the funicular segments are not elongated as in *rabaudi;* third funicular segment length in *oertzeni* lectotype 0.11 mm., width 0.10 mm.

(5) As in *minutus*, the mandibles more massive relative to the remainder of the head and set farther apart from the midline when compared with *umbratus*.

Worker. (Based on a single *oertzeni* syntype and an unlabelled worker in the Mayr Collection). (1) PW of *oertzeni* syntype 0.68 mm., Mayr specimen 0.79 mm., well within range of *umbratus* size variation.

(2) Body hair longer than in *umbratus-rabaudi* but shorter and finer than in *minutus*. In both available specimens the dorsal gastric hairs average about 0.09 mm. and do not exceed 0.14 mm.; the maximum width of the hind tibia at its midlength commonly used in the present study as a reference measurement, is 0.16 mm. The cephalic and gastric hairs of these specimens are sparser than in *minutus*. The number of hairs extending

beyond the profile of the first gastric segment anterior to the extreme posterior strip and seen in perfect side view is 17 in the *oertzeni* syntype and only 6 in the Mayr specimen; 30 or more is usual for *minutus, umbratus-rabaudi,* and *subumbratus.*

(3) Petiolar outline in the *oertzeni* syntype similar to that described for the queen (Pl. 2, Fig. 3); emargination somewhat more shallow in the Mayr specimen.

(4) Scape flattened to the extent seen in extreme *rabaudi* workers. *Oertzeni* syntype: maximum width at scape midlength 0.11 mm., minimum width 0.06 mm. Mayr specimen; maximum width 0.12 mm., minimum width 0.07 mm.

HOLOTYPE. Dr. Bischoff has informed me that the unique type of *bicornis* is not with the Foerster Collection in the Berlin Museum, and it has not been found among the Foerster material in the Mayr Collection. Fortunately, the original description adequately covers the essential diagnostic features in petiole shape and pilosity of this distinctive species, and there can be little doubt that the name has been correctly applied in the present study.

SYNONYMY. The type series of *Lasius bicornis oertzeni* Forel and *Formicina microgyna* Bondroit are nearly identical with one another, as demonstrated in the preceding descriptions. Lectotypes have been selected herein and returned to the collections of the original describers.

Lasius bicornis var. *neapolitana* Emery, as represented in the original description, is separable from *microgyna* only by a trivial difference in the depth of the occipital concavity.

The original description of *Lasius bicornis kashmirensis* Donisthorpe is unfortunately vague, but Donisthorpe does mention two diagnostic characters which seem to place it definitely with this species: (1) the gastric pilosity is very sparse, (2) the petiolar scale matches, with slight differences, that of *neapolitana.* Since *bicornis* is such a distinctive species, I have proposed tentative synonymy for *kashmirensis* as preferable to leaving it a *nomen dubium.*

LASIUS HUMILIS Wheeler
(Subg. *Chthonolasius*)

Lasius humilis **Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston, 52: 528; worker, queen; original description. Type locality: Pyramid Lake, Nevada.**

DIAGNOSIS. A small, pale-colored species known only from a limited area in the southwestern United States.

Queen. (1) The smallest North American *Chthonolasius* known; HW of the three syntype queens measured 1.04, 1.06, and 1.06 mm. respectively.

(2) Scapes longer relative to head width than in any other small *Chthonolasius;* SI of syntypes 85, 88 and 90 respectively, whereas in *umbratus, rabaudi, minutus,* and *bicornis* SI probably never exceeds 82 or 83 and is usually less than 80.

(3) Standing hairs absent from the appendages and sparse on the body. Seen in full face, no more than one or two standing hairs project beyond the entire cephalic contour posterior to the mandibular insertions. Gastric pilosity short and fine; gastric pubescence abundant and completely appressed.

(4) Body and appendages medium yellow, the occiput and thoracic dorsum lightly infuscate.

Worker. This caste by itself may at first be confused with nanitic workers of *L. umbratus,* but differs in the obliteration of the promesonotal impression and in the unusual petiole shape.

(1) Very small; extreme PW range of all series examined 0.53-0.63 mm.

(2) Promesonotal impression seen in side view very feeble or lacking.

(3) Eyes small relative to head; EL range 0.12-0.15 mm.

(4) Dorsal crest of the petiole in frontal view wedge-shaped, tapering upward to form an angular, non-emarginate median prominence.

(5) Body color uniformly light yellow.

LECTOTYPE. By present selection, a queen in the Museum of Comparative Zoology labelled ''Pyramid Lake, Nev. W. M. Mann.'' HW 1.04 mm. Additional syntype queens and workers are in the Museum of Comparative Zoology. A queen and two workers in the T. W. Cook Collection are probably also part of the original type series, despite their differing label ''Pyramid Lake, Nev. 4-6-45.''

DISTRIBUTION. Series from the following localities have been examined during the present study. NEVADA: Pyramid Lake (type series). COLORADO: Salida (W. M. Wheeler leg.; MCZ); 10 miles south of Trinidad, 6500 feet (A. C. Cole leg. and

Coll., MCZ). NEW MEXICO: Tesuque Canyon, Hyde State Park, near Santa Fe, 8700 feet (Cole leg. and Coll., MCZ).

ECOLOGY. Dr. Cole (*in litt.*) has kindly supplied me with the following notes on his Colorado and New Mexico collections. The Trinidad, Colo., colony was found under a stone in the moist soil of a mountain meadow. The Tesuque Canyon, N. Mex., colony was found under a stone in moist, open pine-aspen woods.

LASIUS CRINITUS (F. Smith)
(Subg. *Chthonolasius*)

Formica crinita F. Smith, 1858, Cat. Hym. Brit. Mus., **6**: 13; queen; original description. Type locality: northern India.

Lasius crinitus, Bingham, 1903, The Fauna of British India (Taylor and Francis, London), Hym., **2**: 339–340. (Further description of the holotype.)

Acanthomyops hingstoni Donisthorpe, 1929, Ann. Mag. Nat. Hist., (10) **4**: 448–449; worker; original description. Type locality: Darjeeling, India. NEW SYNONYMY.

DIAGNOSIS. A large, aberrant species known only from the Himalayas. The following diagnosis is based on a single alate queen from Sikkim and three syntype workers of *hingstoni* (all MCZ).

Queen. (1) Largest *Lasius* known; HW of Sikkim queen 1.99 mm.

(2) Pilosity of alitrunk and gaster consisting of extremely long, fine, sinuous, predominantly appressed yellow hairs, which are concentrated along the posterior margin of the pronotum, lateral faces of the scutum, lateral and ventral sides of the first two gastric segments, frontal declivity of the first gastric tergite, and whole surfaces of the exposed posterior gastric segments. They are especially abundant on the posterior gastric segments, converging to form a matted sheath over the apex, but they are sparse over most of the dorsal surfaces of the first two gastric segments and the scutum, and absent altogether from the appendages, the head, most of the pronotum, and all of the propodeum. Similar hairs, many doubled over and wicket-shaped, form a dense fringe along the dorsal crest of the petiole. Shorter, mostly non-sinuous hairs occur on the mandibles and around

the metapleural gland openings. The single specimen examined (Sikkim) is rather badly battered and probably has had some hairs worn off, but its pilosity pattern still agrees generally with that described by Bingham for the holotype.

(3) Scape moderately flattened; in the Sikkim specimen, maximum width at midlength 0.15 mm., minimum width 0.12 mm.

(4) Gastric tergites with abundant appressed pubescence.

(5) Body uniformly ochraceous, the appendages somewhat lighter. The entire body, including the gastric tergites, shagreened and feebly shining to subopaque.

(6) Petiole in frontal view with broadly rounded dorsolateral corners, converging toward the midline to meet a narrow, obtusely angular median excision.

Worker. On the basis of its size, pilosity, petiole shape, and geographic origin, Donisthorpe's species *hingstoni* is considered herein the worker caste of *crinitus.* Three of Donisthorpe's syntypes were used in the following diagnosis.

(1) Exceptionally large; PW 0.88, 0.90, and 0.93 mm. respectively.

(2) Dorsal crest of petiole seen in frontal view wedge-shaped, its sides tapering upward to form an angular, non-emarginate median prominence.

(3) Body pilosity consisting of long, coarse, suberect-erect hairs; maximum length on first two gastric tergites 0.18 mm., on pronotum 0.21 mm., on occiput 0.23 mm. These hairs are concentrated mainly on the occipital margin, pronotum, posterior third of the mesonotum, dorsal convexity of the propodeum, dorsal crest of the petiole, and entire gastric surface; they are occasional over the anterior surface of the head. Appendages completely lacking outstanding pilosity except for a few short, erect hairs on the coxae.

(4) Scapes somewhat flattened, maximum width at midlength 0.13 mm., minimum width 0.08 mm.

(5) Contrary to Donisthorpe's statement, the maxillary palps are not five-jointed, but six-jointed as in other species of *Lasius.*

HOLOTYPE. A queen in the British Museum. From Bingham's detailed description there can be no question about the identity of this exceptional species.

LASIUS CARNIOLICUS Mayr
(Subg. *Chthonolasius*)

Lasius carniolicus **Mayr, 1861, Europäischen Formiciden (Ameisen), p. 51; queen; original description. Type locality: Laibach, Yugoslavia.**

Lasius carniolicus **var. *kusnezovi* Karawajew, 1929, Acad. Sci. Ukraine, Mem. Sci. Phys. Math., 13: 212–213, fig. 5; worker; original description. Type locality: Dau Baba Mountains, Chimkent District, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.**

DIAGNOSIS. *Queen.* (1) The smallest of all the species of *Lasius* in this caste, not exceeding in total size the worker caste; HW of 5 specimens examined (from 5 localities) 0.76, 0.77, 0.77, 0.77, 0.78 mm.

(2) Petiole seen from the side shaped like an inverted U: short, thick, and broadly convex dorsally. In frontal view the dorsal crest broadly convex and non-emarginate. (Pl. 2, Fig. 5).

(3) Mandible relatively small, slender, and delicate, subfalcate with a concave masticatory border and prominent long, narrow apical tooth. Dentition reduced to the apical, subapical, first intercalary, and three basal teeth.

(4) Entire body covered with light yellow standing hairs which rarely exceed 0.11 mm. in length. These are unusual in being abundant over the gular surface and around the entire cephalic margin. Shorter hairs, predominantly decumbent-subdecumbent, occur over all surfaces of the femora and tibiae. Body pubescence everywhere dense, long, and predominantly appressed.

(5) Wings hyaline, unlike those of other *Chthonolasius,* and exceptionally long proportional to the body size (wing length exceeding 4.5 mm.).

(6) Body uniformly medium brown, appendages yellowish brown.

Worker. (1) Petiole seen from the side thick, with a broadly rounded dorsal crest; in frontal view gently tapering dorsally, the dorsal crest convex and non-emarginate.

(2) Eyes set in shallow circumocular depressions and quite small relative to head size; EL 0.11-0.13 mm.

(3) Mandibles more slender than in other *Lasius,* with a reduced offset basal tooth as in *L. sitkaensis.*

(4) The mandibles set closer to the median line than in

other *Lasius;* in frontal view the genal margins (from the anterior borders of the eyes to the mandibular insertions) strongly convex.

(5) Body hairs relatively short and sparse, those on the first three gastric tergites predominantly decumbent. Appendages nearly devoid of pilosity, with only an occasional short decumbent hair along the flexor margins. Body and appendage pubescence dense and predominantly appressed.

(6) Body and appendages medium yellow to very light brownish yellow, the median and posterior areas of the head usually somewhat darker, medium to dark yellowish brown.

(7) Size apparently averaging smaller than in most *Chthonolasius;* extreme PW range of sample studied 0.53-0.60 mm.

Male. (1) Lateral profile of petiole as in worker; in frontal view the dorsal margin is flat to feebly emarginate.

(2) Size small for *Chthonolasius;* HW of single specimen measured 0.83 mm.

(3) Mandibles with numerous irregular denticles along the entire length of the masticatory border.

(4) Moderately long hairs (not exceeding 0.13 mm. in length) abundant over the entire body, including the gular surface and all of the cephalic margin posterior to the eyes. The hairs of the head and alitrunk predominantly suberect-erect, those on the gaster predominantly decumbent. Scapes and tibiae lacking outstanding pilosity; the femora with fairly numerous short standing hairs.

(5) Subgenital plate of the single male dissected differing from that of other *Chthonolasius* in having a relatively straight posterior border, the posterolateral corners not projecting posteriorly. The median posterior setiferous area feebly convex and bearing 6 irregularly placed hairs. The cuspis of the volsella unusually thick, its greatest width exceeding the greatest width of the digitus.

HOLOTYPE. The unique type is in the Mayr Collection. A metatopotype queen borrowed from this collection is typical of the population and has been employed with other specimens in making the above diagnosis.

DISTRIBUTION. *Carniolicus* is widely distributed through most of the Palaearctic Region, although it has never been taken in Japan, England, or North Africa. Following are the records verified during the present study. FRANCE: Drôme, winged queens and males X-1921 (A. Forel leg.; MCZ). SWITZERLAND: Lägern, winged queens X-13-1945 (Kutter Coll., USNM); Monte Generoso (W. M. Wheeler leg.; MCZ); Locarno (Wheeler leg.; MCZ). POLAND: Mosor (D. Müller leg.; MCZ). YUGOSLAVIA: Laibach (Mayr Coll.). KAZAKH S.S.R.: Duany Tau Mountains (N. Kusnezov leg.; MCZ).

The following additional records have been published by previous authors and are probably reliable: Miramount-de-Quercy, France (Vandel, 1926); Visby, Gotland (Forel, 1908); Ponta di Classe, Romagna, Italy (Consani and Zangheri, 1952); Capraia Island, Italy, queen X-1927 (Finzi, 1933); Askole, Karakoram, 3000 meters (Menozzi, 1939). In a distribution map published in 1929 (a), Kuznetzov-Ugamskij indicates records from the following Soviet localities: Kazan; near Sterlitamak in the Urals; the central Caucasus; Abakan, Khakass; the southern Yablonovy Mountains, Chita; Nikolsk-Ussurijsk, Maritime Territory.

ECOLOGY. This species apparently holds its nuptial flights late in the year, since all of the reproductives recorded so far have been collected in October. Kutter (1946) mentions a nuptial flight which occurred at Lägern, near Zurich, at 4 p.m., October 13.

SYNONYMY. *Lasius carniolicus* var. *kusnezovi* Karawajew. This variety, described without direct comparison to specimens of "typical" *carniolicus,* is said to differ by its smaller size, lighter color, and slightly different head shape (less convex genal borders, more convex anterior clypeal border). The first two characters apply to structures which are highly variable in the European population, and on the basis of the description alone they cannot be considered to have taxonomic significance. Judging from Karawajew's figures, the anterior border of the median clypeal lobe of *kusnezovi* is somewhat narrower and the genal borders less convex than in any of the series I have studied, and may be meaningful. Yet the differences seem to fade when compared with the really profound characters which distinguish *carniolicus* as a species. Moreover, the Duany Tau Mountains series, taken in the same general area as *kusnezovi,* shows no significant difference from European series, and Menozzi (1939) could find no differences in his Karakoram material, thus practically eliminating the possibility of *kusnezovi* representing a geographic trend in the Asian population.

Species properly excluded from Lasius

Acanthomyops edwardsi Donisthorpe, 1933, Ann. Mag. Nat. Hist., (10) **12:** 535.

Acanthomyops negrensis Donisthorpe, *ibid.*, p. 537.

Acanthomyops rufo-niger Donisthorpe, *idem*, p. 537.

These three species, originating from Argentina, have already been transferred as synonyms of well known species in the melophorine genus *Lasiophanes* (Kusnezov, 1951).

Lasius eskamole Reza, 1914, Mem. Rev. Soc. Cient. ''Antonio Alzate'' (Mexico City), **44:** 1–22.

The description of this species with the attendant biological notes is nearly unintelligible. Although it may be impossible ever to place *eskamole* to the correct genus (Reza's crude figures are vaguely reminiscent of *Camponotus*), at least it is safe to say that it is not a *Lasius*.

Nomina dubia

The following two species were originally described in *Lasius* but could not be identified on the basis of available descriptions and material.

Lasius terreus Scudder, 1878, Bull. U. S. Geol. Geogr. Surv. Terr., **4:** 747–748; worker; original description. Also, 1890, Bull. U. S. Geol. Surv. Terr., **13:** 618; pl. 10, fig. 23.

(Formicidae) terreus, Carpenter, 1930, Bull. Mus. Comp. Zool., **70:** 19.

This species was described from the Green River shales of Wyoming (middle Eocene). According to Carpenter, the unique type is too poorly preserved to allow generic placement.

Acanthomyops (Donisthorpea) kosswigi Donisthorpe, 1950, Ann. Mag. Nat. Hist., (12) **3:** 638; worker, queen; original description. Type locality: Kars, Turkey. Location of types: British Museum (Natural History).

Donisthorpe's description contains nothing which even hints at the relationship of this species to other members of the genus. Until the types can be examined again, even the subgeneric placement will remain a guess.

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Ant Genus *Lasius*

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[1] *Lasius* (*Formicina*) *flavus claripennis* Wheeler, 1917, Proc. Amer. Acad. Arts Sci., 52 :527, worker, female, male. Synonymized with *L. flavus microps* Wheeler by Creighton, 1950, p. 422.